National Park Service
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*Annual Report for the Central Alaska Network Vegetation Monitoring Program 2008*

Natural Resource Technical Report NPS/CAKN/NRTR—2010/382

**ON THE COVER**
Alaskan *Picea glauca* (white spruce) cone
Photograph by: Carl Roland

# White spruce cone and seed production in relation to climate in the Rock Creek watershed of Denali National Park and Preserve during the period 1992-2007

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Natural Resource Technical Report NPS/CAKN/NRTR—2008/XXX

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# Executive Summary

The National Park Service has monitored the annual growth and reproductive output of white spruce trees in six replicate plots at two sites in Denali National Park and Preserve since 1992. White spruce is the primary treeline species in Denali and thus changes in growth and reproductive rates of this species over time may result, over time, in shifts in the location of treeline on the Park landscape. Such shifts would have major ecological consequences, including important changes in the structure and productivity of the vegetation, alterations in the frequency and distribution of fires, and changes in important attributes of bird and mammal habitat.

The sampling design for this program includes three identical replicate plots in each of two sites: the "Forest" site and the "Treeline" site. The plots were 50 m x 50 m square with an internal 25 m x 25 m subplot in which most of the observations were made. There were six white spruce trees for which cones counts were recorded in each of the three replicate plots at each site (thus n = 3 plots per site, each with n = 6 trees). The mean values presented here were derived by averaging over the three mean values for each replicate plot in each "site" in the design (that is the "Forest" site and the "Treeline" site). There were also six 0.25 $m^2$ seed traps placed in each of the three replicate plots for each site. The mean number of seeds per trap was derived by taking the average of the means for each of the three plots at a site (n = 3 plots). I compared selected results from this monitoring program to similar monitoring activities that have occurred in the Bonanza Creek Long Term Ecological Monitoring site near Fairbanks, Alaska.

In this report I present the results of this long term monitoring program for the period 1992 – 2007, and place the results in the context of annual variation in important climate variables that are thought to affect white spruce growth and reproduction. I summarized values for climate variables from observations made daily at the Kennels weather station at Denali National Park and Preserve headquarters for this period of time. The following variables were measured there: daily minimum and maximum temperature, snow depth, daily precipitation sum (snow and water equivalent).

The values for mean daily temperature across the growing season (April – August) for the years 1992-2007 varied between a low of 6.37° C in 2000 and a high of 10.68° C in 2004. The average across the entire period was 8.11° C (± 0.32° C). Four years during this period had an average April through August daily average temperature over 9 degrees (1993, 2004, 2005, and 2007) and four years had an average temperature of less than 7° C (1992, 1996, 2000, and 2006). Based on the Rock Creek kennels weather station data, the three warmest growing seasons (as measured by the sum of heating degree-days accumulated post-snow free date in the period April – August) observed over the measurement period occurred in the last four years (2004, 2005 and 2007). 2004 and 2007 were also lower-than-average for the period in terms of growing-season precipitation sums.

Annual cone production of white spruce trees in both Rock Creek study sites (Forest and Treeline) was extremely variable among years, with a few highly productive years and the majority of years with negligible cone production during the measurement period. In 1998 both spruce monitoring sites in the Rock Creek study area had banner cone crops.

The average number of cones per tree in white spruce was higher, on average, in the Forest site than in the Treeline site over the sampling period: 71.2 ± 27.2 vs. 41.9 ± 11.2 respectively.

However, in two recent warm summers (2004 and 2005) we observed higher mean cone productivity per tree in the trees at the Treeline site as compared to the trees in the Forest site.

There was a relatively strong positive correlation in the pattern of annual variation in mean number of cones per tree ($r = 0.793$) between the Forest and Treeline sites reflecting a general synchrony in cone productivity of trees in these two landscape positions.

In the years 2004 and 2005 we recorded high levels of cone production by white spruce trees in the Treeline site, but well below-average cone production for trees in the Forest site. This suggests different limiting factors may be operating on the trees at the two sites. Interestingly, 2004 was the warmest year in the period by all measures (average temperature and degree-day accumulation). It is possible that the lowland Forest sites, which were more densely forested, experienced a density-dependent drought stress as a result of this long, dry summer growing season. Treeline sites supported much less dense stands and thus less competition among individual spruce trees.

These results appeared to conform to the pattern of above-average cone crops being initiated in response to warm, dry conditions in the early growing season (June) that has been documented in the literature. Specifically, for the Forest site above-average cone crops were initiated in 1997, 1999, and 2001 – all years with higher than average June daily temperatures and below-average June precipitation. For the Treeline site, above-average cone crops were initiated in the years 1997, 1999, 2003, and 2004. During each of these years, the Park headquarters area experienced both below-average precipitation and above-average temperatures except during 2003, which was the third driest June over this period, but experienced below average daily maximum June temperatures.

As expected, the relative abundance of cones in a given year was strongly positively correlated with seed rain for the Forest site, as measured by the seed traps. A similar correlation (although weaker) was observed in the Treeline site. It is likely that redistribution of seeds by wind is a source of bias in our estimate of relative seed production for the Treeline site.

Overall, the average number of white spruce seeds per seed trap was consistently much higher and more variable in the Forest site as compared to the Treeline site across the study period: 71.5 seeds/trap/year ± 31.4 in the Forest site versus 4.4 seeds/trap/year (± 1.4) in the Treeline site.

We observed a strong degree of synchrony in the patterns of annual variation in white spruce seed rain in white spruce trees in the Rock Creek Forest site and those in the floodplain white spruce forest site in the Bonanza Creek experimental forest (near Fairbanks) over the period 1992-2003. This is strong evidence that patterns in white spruce seed production are very large in scale, perhaps synchronous over much of interior Alaska, at least among trees located in similar landscape positions.

Annual estimates of relative spruce seed viability (germination percentage) varied over the period, but in a manner out of phase with cone and seed productivity. The highest mean annual germination percentages of white spruce seeds were recorded in 1997 and 2002 in the Forest site

(31% ± 7%, and 28% ± 4% respectively). For the Treeline Site, the highest mean annual germination percentage was recorded in 2005 at 23% (± 6%).

The estimates of mean annual seed viability across the entire period were considerably higher in the Forest than the Treeline site. We observed an overall mean of 9 % seed viability over the period for the Forest site and just 4 % mean viability in the Treeline site over this period.

The inter-annual patterns in the relative viability of white spruce seeds among years were generally synchronous between the Rock Creek Forest site and Bonanza Creek floodplain forest study areas during the period 1992-2003 with the exceptions of the cool summers of 1992, 1998, and 1999, in which the relative seed viability observed in the lowland Bonanza Creek area was apparently considerably higher, on average, than in the Rock Creek Forest site. Overall, mean seed viability was marginally higher in the Bonanza Creek site as compared to the Rock Creek Forest site.

In general, the pattern in seed viability within this data set suggests decreasing mean seed viability with increased site elevation with the following order: Bonanza Creek floodplain > Rock Creek Forest > Rock Creek Treeline. This likely reflects the influence of season length and warmth (degree-day sums) in producing viable seed crops at this latitude. However, in particularly warm years such as 2004 and 2005, the percent viability of the seeds collected from the Treeline site may approach the levels observed in the other two sites.

The largest mean number of viable seeds per unit area per year in the Forest site were observed in 2002 (54 viable seeds per trap 0.25 $m^2$), 1998 (28 viable seeds per trap) and 1997 (14 viable seeds per trap). The overall mean for annual numbers of viable seeds produced per trap was 9 ± 4.38 for the Forest site and 0.4 ± 0.27 for the Treeline site. Significantly, 1998, the year in which the largest mean annual production of white spruce cones and seeds were recorded in both Rock Creek monitoring sites was not the year during which the largest number of viable seeds were produced in these sites. In contrast, the highest mean annual viable seed production in the Forest site was recorded in 2002, the wettest year on record and the highest mean annual production of viable seeds in the Treeline site occurred in 2005 the second year of the warmest two-year period during the study.

Comparison of annual variations in white-winged crossbill counts with annual seed rain data from the Forest site showed a strikingly high degree of synchrony between these two variables during the course of this study. The results of this 16 year monitoring program provide a dataset that illuminates one strand of the multi-trophic level set of interactions within the boreal ecosystem of interior Alaska over nearly two decades. This dataset includes the information about the influence of climate in causing annual variations in reproductive effort in white spruce, and the consequences of these variations for white-wing crossbills, a species dependent on spruce seeds for sustenance. This set of baseline of information will allow us to understand the potential perturbations to these ecosystem relationships that may occur due to warming climatic conditions in the boreal regions which will likely have profound influences on each level of this food chain.

# Introduction

White spruce (*Picea glauca*) is the primary treeline tree species in Denali National Park and Preserve. Consequently, changes in the growth and reproductive rates of this species over time may result in shifts in the location of treeline on the Park landscape. Such shifts would have major ecological consequences, including important changes in the structure and productivity of the vegetation, alterations in the frequency and distribution of fires, and changes in important attributes of bird and mammal habitat. Due to its importance within the ecosystem, primary aspects of white spruce growth and reproduction have been monitored since 1992 as a part of the Long Term Ecological Monitoring program in Denali (initially) and currently as part of the Central Alaska Network vegetation monitoring program.

In this report I summarize the results of the white spruce monitoring activities performed in the Rock Creek watershed during the 16-year period 1992-2007. In addition, I describe the variation of fundamental climate variables that have affected spruce growth and reproduction during the course of this study. For comparison, I present selected results of white spruce monitoring data for the same period from the Bonanza Creek LTER site near Fairbanks, located in the lowlands north of the Park. In addition, I provide summaries of small mammal and resident bird observations that occurred in the Rock Creek area over the same period of time, and briefly explore the potential relationships between white spruce reproductive effort and population levels of these species.

The following annual monitoring activities relating to white spruce occur in the study area: 1) annual records of spruce cone production and annual growth increment from a randomly-selected subset of trees within the permanent vegetation plots in the Rock Creek watershed near Park Headquarters; 2) annual estimates of seed rain from seed traps within the same permanent plots; and 3) annual germination trial experiments that were carried out with white spruce seeds collected from these seed traps each year.

This program has monitored white spruce growth rate and reproductive effort in replicate plots at a forested site ("Forest") and a higher elevation treeline site ("Treeline") in the Rock Creek watershed of Denali National Park annually since 1992 (see Densmore 1997). These plots are arranged on an elevation gradient that also includes plots in the tundra well above treeline. The objective of this monitoring program is to detect inter-annual variation and long-term trends in spruce cone and seed production and annual bole growth over time. We also seek to monitor the relationships between climate variables and spruce growth and reproduction in our study populations in order to understand the effects of these causal variables on important aspects of spruce biology.

Although this document constitutes the annual report for the entire Central Alaska Network Vegetation Monitoring Program, I focus on the results of white spruce monitoring in the Rock Creek study area of Denali over the period 1992-2007. Due to space and time constraints, I omit presentation of the other work that the program that accomplished in 2007. In addition to the limited set of activities that occurred in the Rock Creek plots, the CAKN vegetation monitoring program also completed fieldwork for the landscape-scale vegetation monitoring program in eleven mini-grid study areas during the 2007 field season in three network parks. This work included installing and measuring 163 vegetation plots in seven study areas in Denali and installation and measurement of 80 permanent vegetation plots in four study areas in the other two network parks: Wrangell-St. Elias National Park and Preserve, and Yukon-Charley Rivers National Preserve. The results of this work will be presented and discussed in detail in future reports.

# Methods

The sampling design and methods used for this program were described in detail in the protocol document (Densmore et al 1997). I summarize the relevant sampling design and methods used for white spruce monitoring briefly here. The plot layout and arrangement, and the parameters monitored within the plots were modeled on the permanent vegetation plot design for the Bonanza Creek Long Term Ecological Monitoring site near Fairbanks (see http://www.lter.uaf.edu/bcef/exp_design.cfm).

### Study area and sampling design

The study area is located in the Rock Creek watershed near park headquarters in Denali National Park and Preserve (see Fig. 1 for map). This watershed drains the southern flanks of Mt. Healy and encompasses the transition from mature white spruce-paper birch forest in the creek bottom to exposed alpine tundra on the ridges, including large areas of closed tall alder scrub and open white spruce woodland in the subalpine zone. The locations of the monitoring plots were selected to capture the lowland forest and open spruce woodland at treeline for monitoring attributes of white spruce growth and reproduction. The plots were chosen to represent an elevation gradient and typical “lowland” and “treeline” plant communities. Plots in the Forest site are located at approximately 730 m elevation in the valley bottom, and the plots at the Treeline site span elevations of 940 to 980 m on a broad ridge to the west.

The sampling design for this program includes three identical replicate plots in each of two sites: the “Forest” site and the “Treeline” site (see Fig. 2 for plot diagram). The plots are 50 m x 50 m square with an internal 25 m x 25 m subplot in which most of the observations were made. There were six white spruce trees for which cones counts were recorded in each of the three replicate plots at each site (thus n = 3 plots per site, each with n = 6 trees). The mean values presented here were derived by averaging over the three mean values for each replicate plot in each “site” in the design (that is the “Forest” site and the “Treeline” site). There were also six 0.25 $m^2$ seed traps placed in each of the three replicate plots for each site. The mean number of seeds per trap was derived by taking the average of the means for each of the three plots at a site (n=3 plots). Representative photographs of the monitoring plots are shown in Plate 1.

The seed traps were set out each year in mid to late August and lined with muslin fabric. The traps were collected in May each year and the contents sorted – all white spruce seeds were tallied and placed in a seed envelope and into a freezer for storage. In the fall, we performed germination trials on the white spruce seeds collected from each of the traps (Densmore 1997). The number of germinated seeds from each seed trap was recorded to determine the viability (percent germination) of each year’s seed crop. The methods used for this program are identical to those used at the Bonanza Creek Experimental Forest LTER site near Fairbanks, which allows direct cross-comparisons of the data from these two study areas.

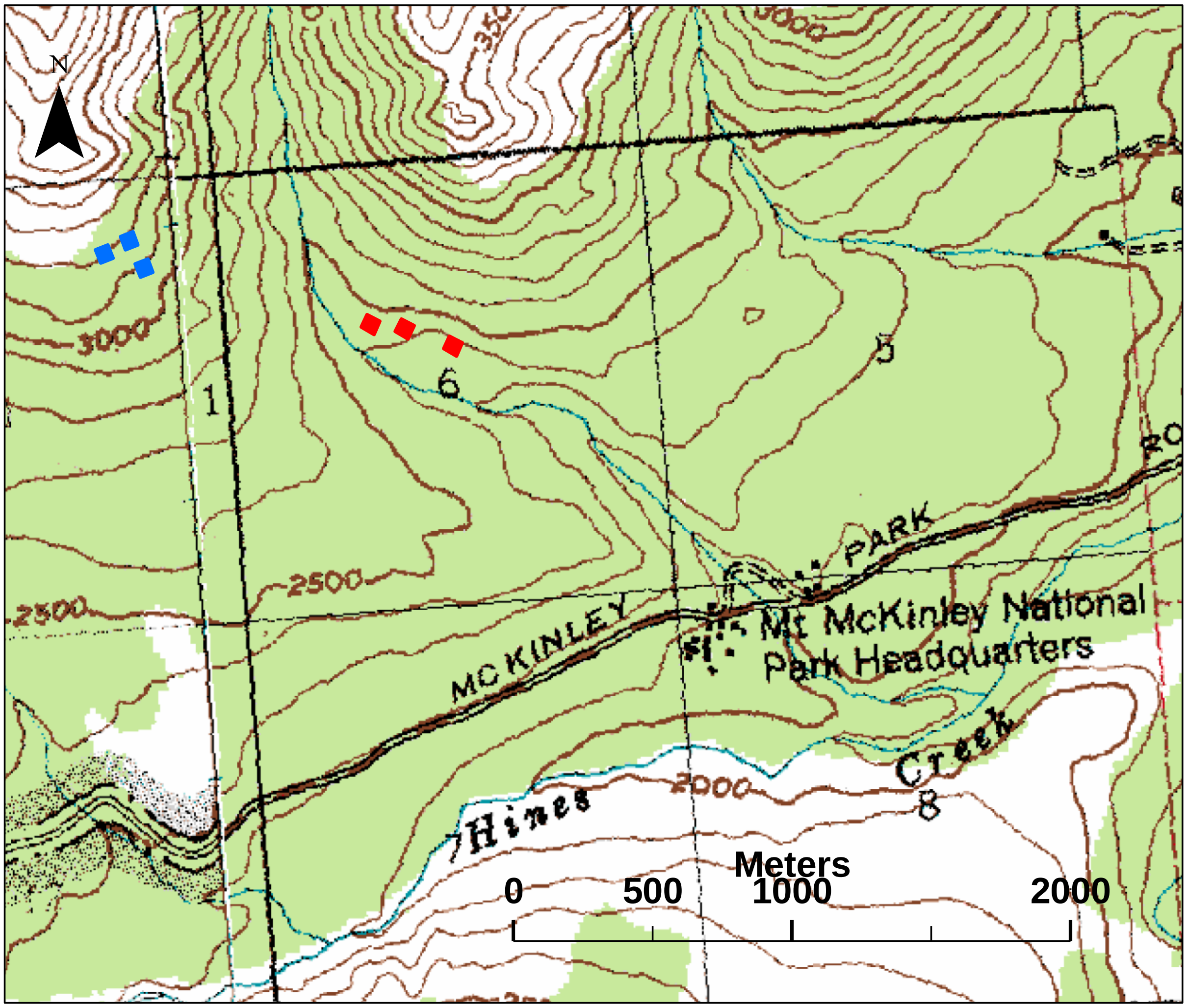


Figure 1. Map showing the location of the Rock Creek watershed long term monitoring plots where observations of white spruce growth and reproduction have been made. The red squares indicate location of the Forest site (3 replicate plots) and blue squares show the location of the Treeline site (3 identical replicate plots). Contour map shows elevation in feet.

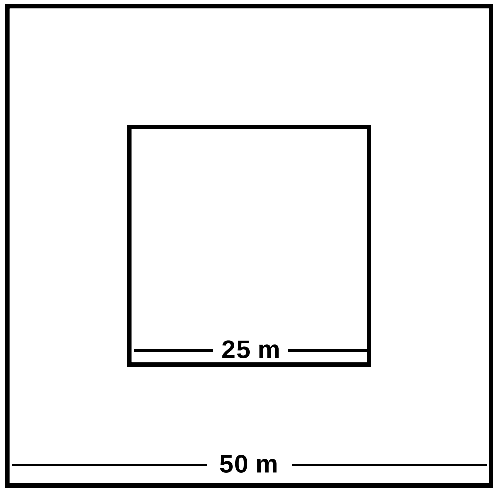


Figure 2 Schematic drawing showing the plot design for the Rock Creek watershed long term monitoring study plots.  Measured spruce trees are located in interior 25 m x 25 m plot, and seed traps are located in the outer section of the 50 m x 50 m plots.


Plate 1.  Four photos of the Long Term ecological monitoring plots in the Rock Creek watershed; A) Forest plot #1 B) Forest plot #2; C) Treeline plot #2; D) Treeline plot #3.

### *Cone counts and dendrometer bands*

Five trees were randomly selected from each of the interior 25 m x 25 m subplots for cone counts to monitor the number of cones produced per tree over time. The numbers of mature spruce cones produced per tree were estimated by making direct counts of cones that would mature in the current-year from the ground using binoculars. For large trees (including all the trees in the Forest site), all cones were counted from one side of the tree and this number was multiplied by two to get an estimate for the whole tree. For small trees for which it was possible to keep track of all the cones counted without double counting or missing cones (most of the individuals in the Treeline site) we counted all cones visible for each sample tree.

To monitor annual growth increment of spruce, the five selected trees (of sufficient size) were fitted with dendrometer bands in 1992. Five trees per replicate plot were banded in the Forest site. In the Treeline site where trees were less dense and smaller, there were not enough trees of sufficient diameter to deploy five dendrometers per replicate – instead, Treeline plot #1 contained three dendrometer trees, plot #2 contained four dendrometer trees and plot #3 had only one tree of sufficient size to be fitted with a dendrometer band. The focus of this report is on the cone and seed data and I do not report the dendrometer results here.

### *Seed rain and seed viability*

As described above, six 0.25 $m^2$ muslin-lined seed traps were placed in each replicate plot in both sites each August to sample the seed rain in these plots. The muslin linings containing litterfall and seeds traps were removed in May each year and the contests sorted. The number of white spruce seeds was counted and the seeds placed into envelopes (all seeds from one seed trap per envelope) and stored in a freezer. Seeds were removed from the freezer and germination trials were performed to determine the numbers of viable seeds per seed trap and germination percentages for each plot for each year (see Densmore 1997). Estimates for annual seed rain per unit area were derived in a similar fashion to the tree parameters – mean for each replicate across six traps, and n=3 replicates for each site. Estimates of the number of viable seeds per unit area were also estimated for each site after the germination results were compiled.

# Results

## Variation in climate variables over the measurement period

I summarized values for climate variables from observations made daily at the Kennels weather station at Denali National Park and Preserve headquarters for this period of time. The following variables were measured there – daily minimum and maximum temperature, snow depth, daily precipitation sum (snow and water equivalent). For purposes of this report, I focus on growing-season climatic conditions for the months of April through August.

### *Precipitation and snow depth*

Total growing-season precipitation (April through August) at park headquarters varied substantially over this period – from a low of 17.4 cm in 1993 to a high of 43.9 cm in 2002 (Fig. 3). The mean total annual growing season precipitation across the period was 23.8 cm (± 1.6 cm). There were six years with precipitation totals exceeding 25 cm over the April through August period (1997, 1998, 2000, 2002, 2005, and 2006) and four years with less than 20 cm of total growing season precipitation (1992, 1993, 1996, and 2004).

Average snow depth on the ground in April and May at the kennels weather station was also variable over the measurement period, as a result of large variations in the amount of cumulative snowfall over the season and the different trajectories of spring snowmelt across the years in the measurement period (Fig. 4). The mean daily snow depth for the month of April across all years was 46.7 cm per day (± 5.3 cm). The maximum value was 91.5 cm per day in the high snowpack year of 1993, and the lowest value was 2.9 per day in 2003, resulting in a range of 88.6 cm for this average April snow depth over the period. The highest mean daily snow depths for April (in excess of 60 cm/day) were recorded in 1992, 1993, 1996, and 2000 whereas the lowest mean daily snow depths (less than 35 cm/day) occurred in 1998, 1999, 2003 and 2007 (Fig. 4).

The mean daily snow depth for the month of May across all years was 10.3 cm per day (± 3.5 cm). The maximum value was 41.2 cm per day in both 1992 and 1996, and the lowest value was 0 cm per day in 2003, for a range of 41.2 cm/day for this variable over the period. The highest mean daily snow depths for May (in excess of 20 cm/day) were recorded in 1992, 1996, and 2000 whereas the lowest mean daily snow depths (less than 1 cm/day) occurred in 1994, 1995, 2003-2005 and 2007 (Fig. 4).

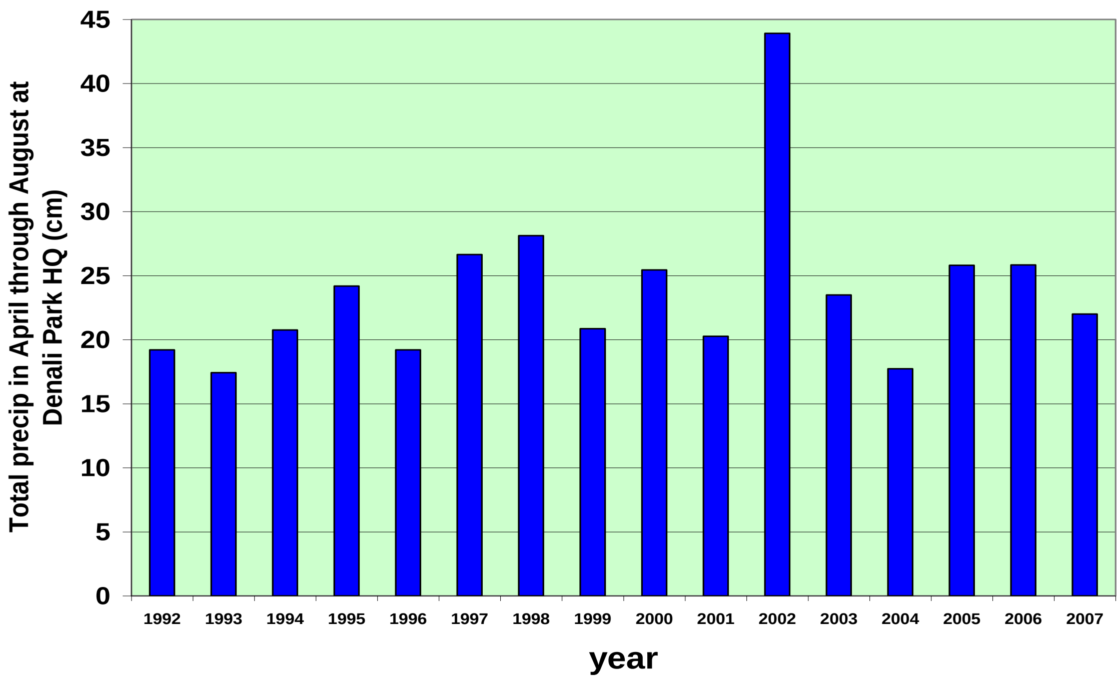


Figure 3. Total precipitation during the period April 1 – August 31 at Denali Park Headquarters, Alaska weather station during the period 1992 – 1997 (cm).

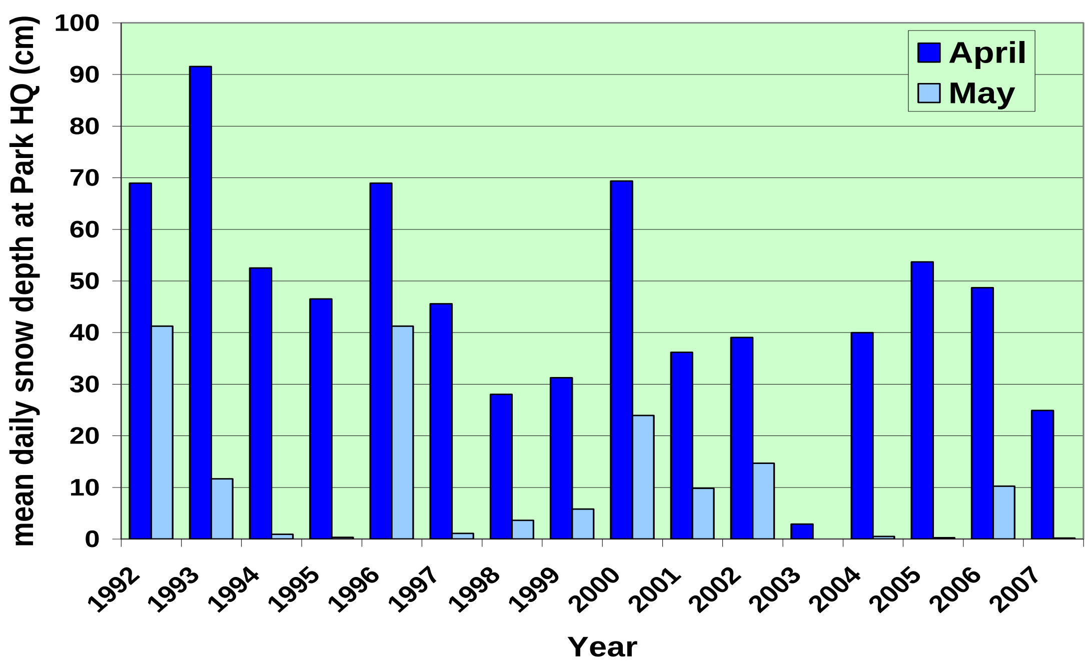


Figure 4. Mean daily snow depth for the months of April and May at Denali Park Headquarters weather station during the period 1992-2007 (in cm).

### ***Snow free days***

I calculated the number of snow free days for April and May for each year from 1992 to 2007 (Fig. 5). Snow-free date is important because this point in time represents a qualitative shift in the radiation regime for the soil surface when direct solar radiation begins to reach and directly warm and thaw the ground. Snow-free date is related to both the depth of the snowpack accumulated over the winter, and the tempo of spring snowmelt. As such, years with early snow-free dates can be markedly different in relation to important plant-growth and phenology-related variables depending on whether it was a low-snow year or snowmelt occurred early.

The only year in which snow-free days were observed in the month of April was 2003 when there were 17 days with no snow on the ground at Park headquarters during April (Fig. 5). The mean number of snow free days in May at Park headquarters over this period was 21.4 (± 2.1 days). 1992, 1996, and 2000 were the only years in which 10 or fewer snow-free days were recorded, and 2003 and 2007 were the only years where there 30 or more snow-free days recorded in May.

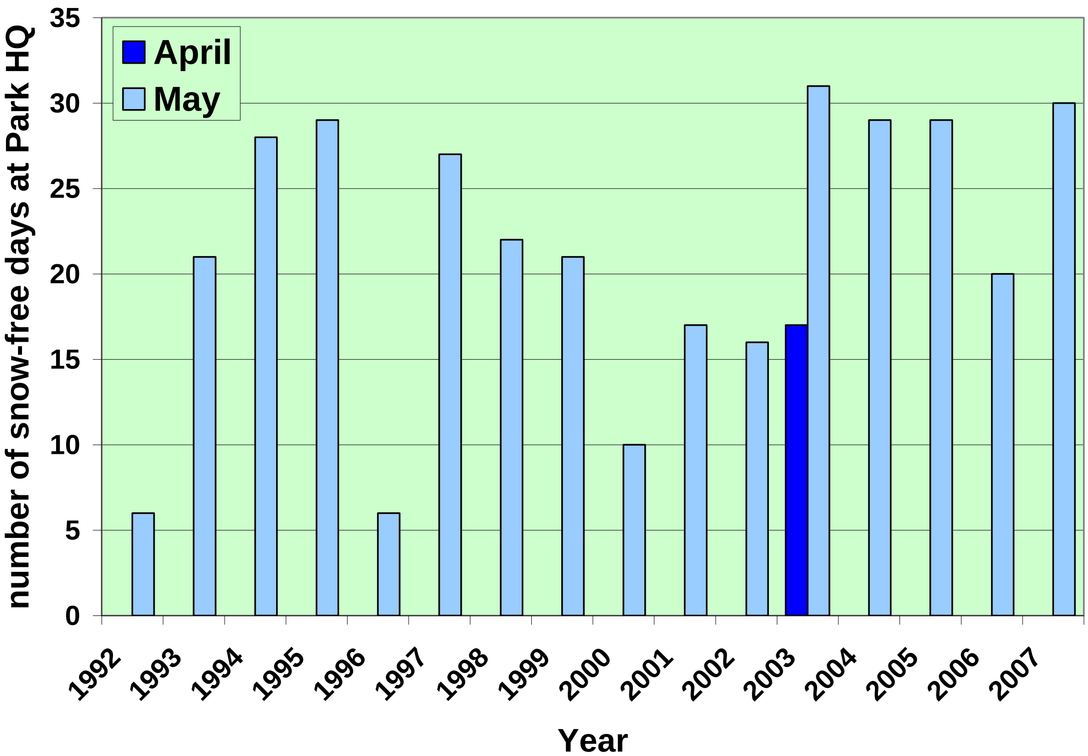


Figure 5. The total number of snow-free days observed at Park headquarters weather station in April and May over the period 1992 -2007.

### ***Temperature and degree-day accumulation***

The values for mean daily temperature across the growing season (April – August) for the years 1992-2007 varied between a low of 6.37° C in 2000 and a high of 10.68° C in 2004 (Fig. 6). The average across the entire period was 8.11° C (± 0.32° C). Four years during this period had an average April through August daily average temperature over 9 degrees (1993, 2004, 2005, and 2007) and four years had an average temperature of less than 7° C (1992, 1996, 2000, and 2006).

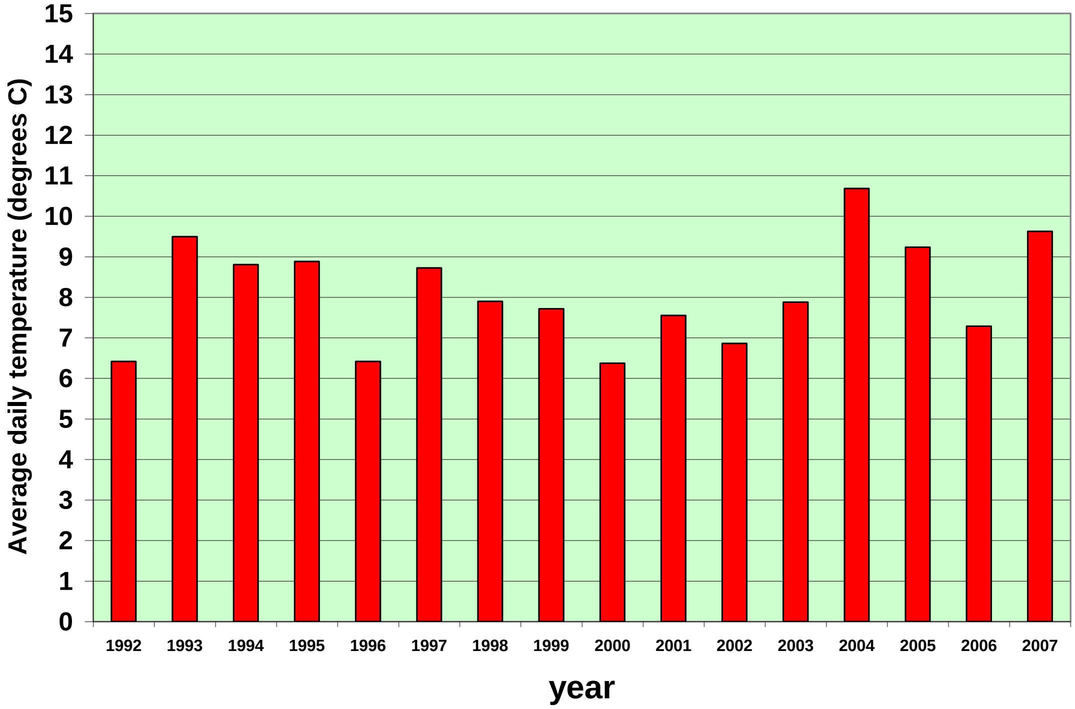


Figure 6. Mean daily temperatures recorded at the Denali Park Headquarters weather station during the months April through August for the period 1992 – 2007.

Mean daily temperature is often not the most biologically informative measure of temperature. The accumulation of degree days over the growing season represents cumulative warmth over time above a threshold value and is frequently used to predict the timing of biological events. Figure 7 shows the patterns of variation in heating degree-day accumulation across the period 1992- 2007. The total accumulated heating degree days following snow-free date for the period April – August (the sum of daily average temperatures > 2 degrees C across the period once snow depth = 0 at the Kennels weather station) varied from a low of 1009.4 DD in 2000 to a high of 1618.5 DD in 2004. In general, the warmest growing seasons (for the entire April – August period) during this period occurred in 1993, 2004, 2005 and 2007 whereas the coolest growing seasons occurred in 1992, 1996, 1998 and 2000.

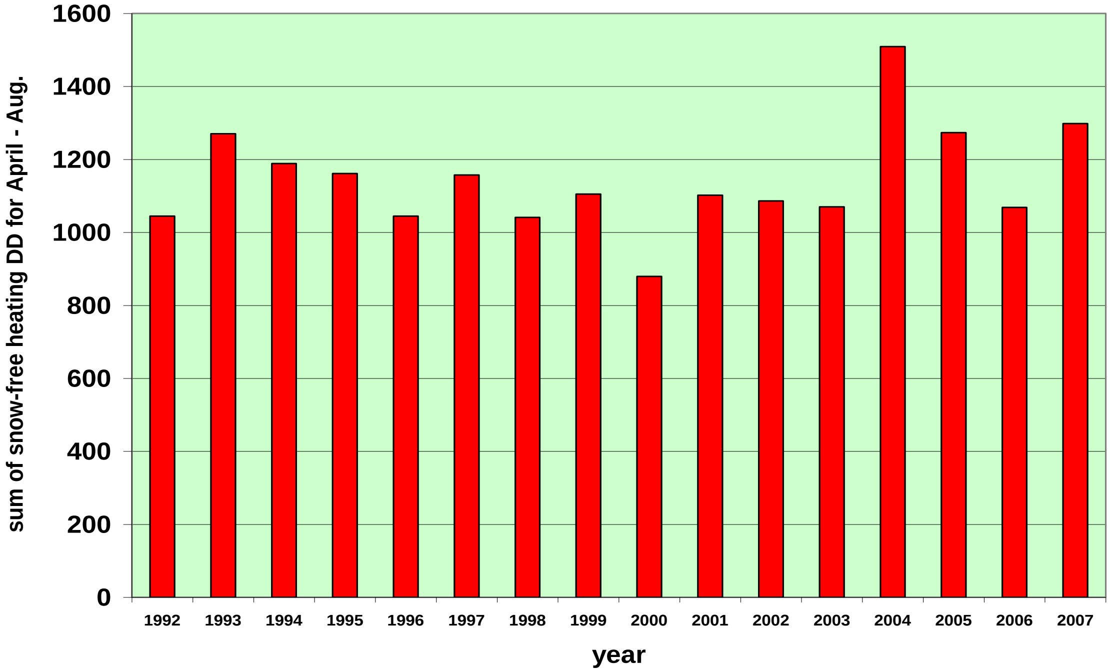


Figure 7. Total accumulation of heating degree days for the period April – August following snowmelt for the years 1992-2007. One degree day equals each degree of average daily temperature over the minimum threshold of 2 degrees, thus for a day with an average temperature of 3 degrees, one degree-day is added to the total. Degree days that were accumulated prior to the snow-free date were not counted for this analysis.

In order to examine the covariation between temperature and precipitation, I standardized total annual precipitation and mean daily temperature by their respective period annual means for each year during the measurement period (Fig. 8). Seven years showed greater than average April- August precipitation. Of these, only 1995, 1997, and 2005 also showed greater than average mean daily temperatures for the period. The mean temperature for 2002, which had the highest precipitation over the period (184.5% of the overall mean precipitation for the period), was only 84.5% of the period mean. The precipitation for 2004, on the other hand (which had the highest temperature over the period (134.7% of the period mean) was only 74.5% of the period mean for annual total precipitation (Fig. 8). In general, then, there was an inverse correlation between growing season precipitation and heating degree days sums during the period 1992 through 2007 ($r = 0.323$; see Fig. 9).

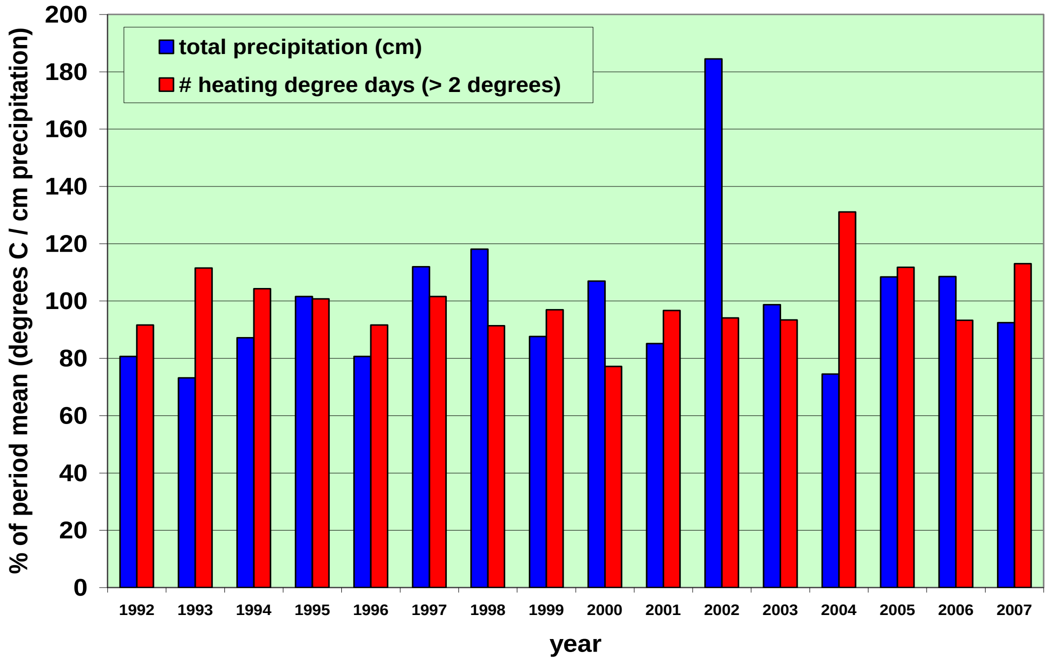


Figure 8. Standardized observations for cumulative precipitation and mean number of heating degree days calculated from daily temperature records from Denali Park headquarters weather station. The bar heights represent the percentage of the overall mean value for the entire period that were recorded for each year. For example, precipitation was more than 180 percent of the mean in 2002.

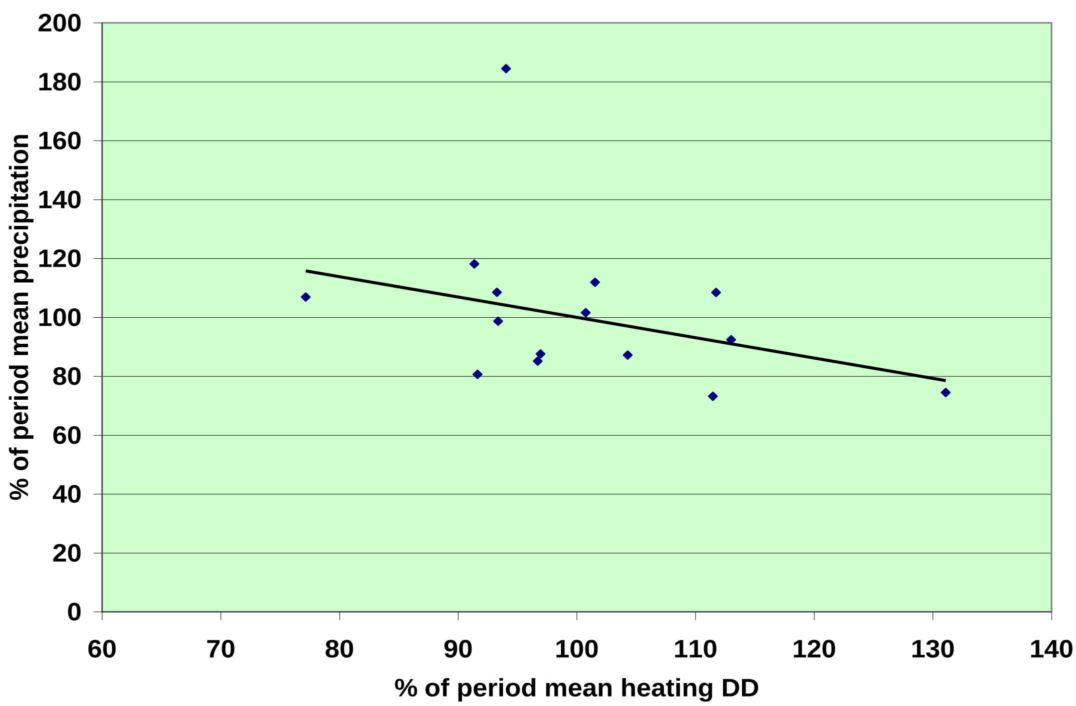


Figure 9. The relationship between standardized value for heating degree days over the growing season and standardized total precipitation over the growing season for the years 1992 – 2007. Note the inverse correlation between the two variables.

## White Spruce reproduction

### *White spruce cone crops*

Average cone production per tree in the Forest site over the measurement period ranged from a low of zero, which was observed in three different years (2003, 2006 and 2007) to a high of 390 (± 59) in the banner cone year of 1998 (Fig. 10). The average number of cones per tree per year across all of the 16 years of measurements in the Forest site was 71.2 cones per tree (± 27.2). Figure 11 presents the cone production results for the Forest site as annual deviations from the grand mean cone production per tree over the entire period for the site. This histogram shows that in only four of the sixteen years did the trees show cone production greater than the overall mean for the period (1992, 1998, 2000, and 2002).

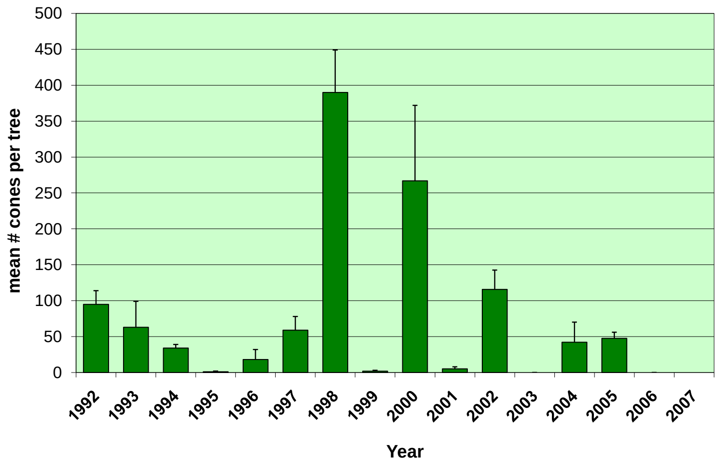


Figure 10. Mean number of cones per tree recorded in the Forest site of Rock Creek watershed over the period 1992 – 2007 (± 1 se).

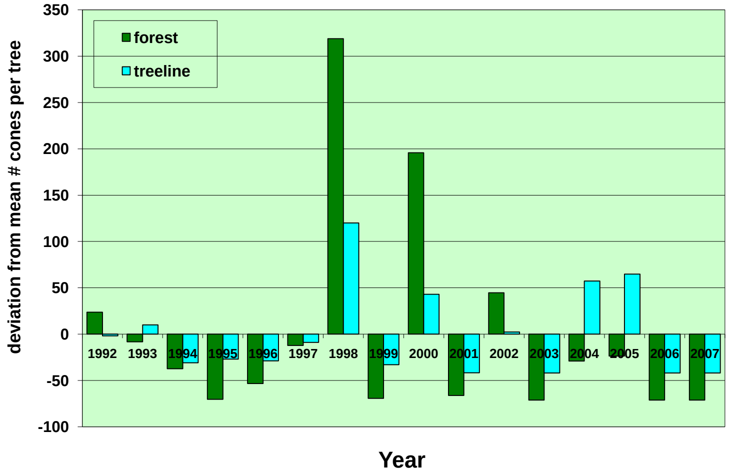


Figure 11. The mean number of white spruce cones produced per tree in two sites in Denali National Park, presented as deviations from within-site grand mean over the entire period (thus the value on the y-axis represents the mean of current year cone production for the site minus the overall mean of cone production for the site over the entire measurement period. Positive values represent years with greater than average cone production).

Average cone production per tree in the Treeline site over the measurement period ranged from a low of zero, which was observed in 2003, 2006 and 2007 to a high of 162 (± 49) in 1998 (Fig. 12). The average number of cones per tree per year across all of the 16 years of measurements in the Treeline site was 41.9 cones per tree (± 11.2). Figure 11 presents the cone production results for both sites as annual deviations from the grand mean over the period. This histogram shows that in only five of the sixteen years did the trees in the Treeline site show a mean cone crop greater than the overall mean for the period (1993, 1998, 2000, 2004 and 2005).

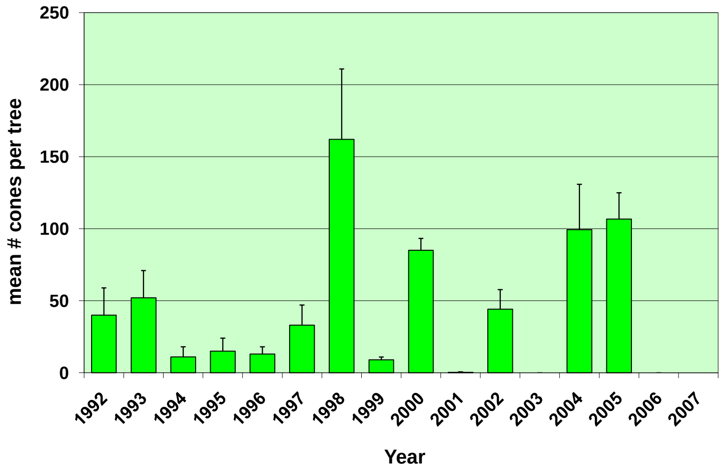


Figure 12. The mean number of cones produced by trees in the Treeline site of Denali National Park on an annual basis over the period 1992 – 2007.

In absolute terms, the mean annual cone production of trees in the Treeline site was lower over this measurement period than the mean for trees in the Forest site (a mean of 71.2 cones per tree for the Forest site and 41.9 cones per tree in the Treeline site). This difference was likely due to the much larger average size of the trees in the Forest site, which gives them an increased capacity to produce cones in any given year as compared to the smaller trees in the Treeline site. The correlation coefficient between the values for the annual mean number of cones per tree at the two sites over the period was $r = 0.793$ (see Fig. 13), which reflects a general synchrony in the relative means for cone production between these two sites. Interestingly, however, only two of the above-average cone production years at the Treeline site occurred in the same years as above-average cone production was also observed at the Forest site (1998 and 2000), whereas three of these five above-average years were different among the two sites (1993, 2004, and 2005). This result suggests that different limiting factors may be driving annual variation in cone production in the spruce trees at these two sites during certain years (Fig. 11).

There were two conspicuous exceptions to the general synchrony of annual cone production between the Forest and Treeline sites over this period, which occurred in 2004 and 2005. In both of these years, cone production in was above the period average in the Treeline sites , but below average for the Forest site (Fig. 13). These cone crops were initiated in 2003 and 2004 respectively, which were both years with below-average precipitation. Both of these years were remarkable for early-season weather in that 2003 experienced by far the earliest snow-free date and lowest average late-season snowpack during the period and 2004 had the warmest June temperatures over the entire period by a large margin.

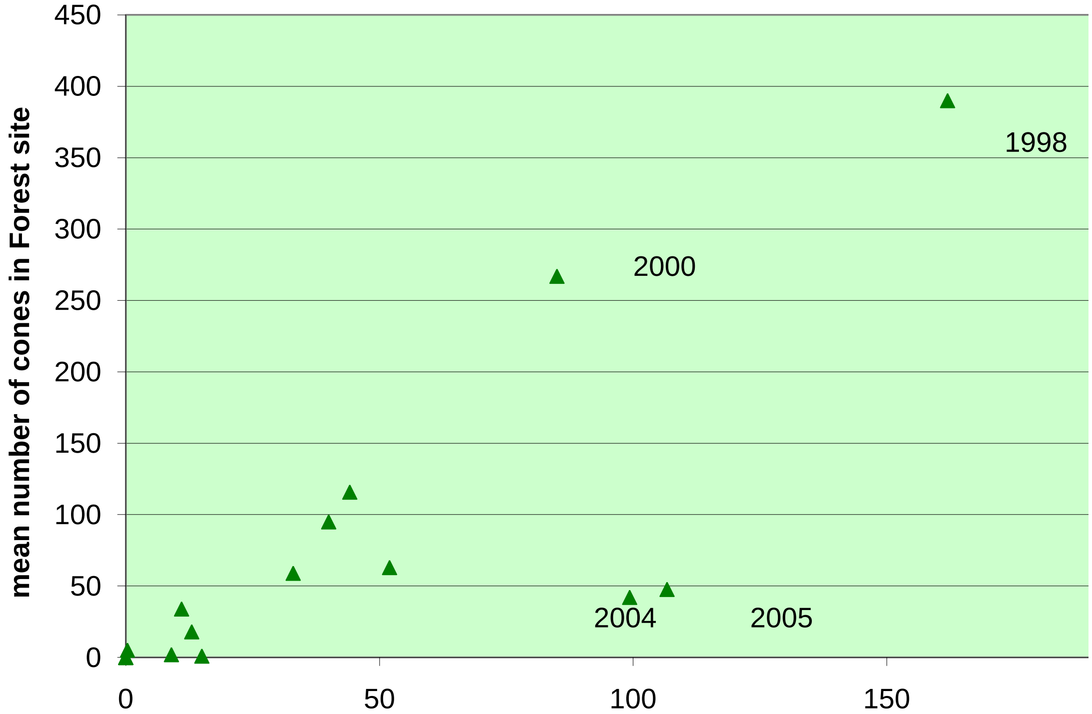


Figure 13. A scatter plot showing the relationship in mean annual cone production per tree in the Forest and the Treeline site for the period 1992 through 2007 (the points representing the years 1998, 2000, 2004 and 2005 are labeled. Note the strong correlation among these pairs of values except for the years 2004 and 2005.

***Relationships between annual cone crops and climate parameters***

Cone production in white spruce is initiated in the year prior to fertilization and maturation of the seeds. It is thus a two-year process to produce mature white spruce cones with fertile seeds. Female cones are initiated and grow to a button stage in one year and then become fertile and reach maturity the following summer. The climatic factors that are associated with initiation of large numbers of cones are above average temperatures and below average precipitation in the early growing season (Fraser 1958 and Matthews 1963).

To investigate the relationship between these factors and cone production in the Rock Creek study area, I calculated mean June temperature and mean cumulative June precipitation for each year during this period. The histogram in Figure 14 shows the deviation of each annual value from the period mean for June temperature.  Note that the years 1993, 1997, 1999, 2001, 2004, and 2005 all had above average June daily temperatures. Figure 15 shows the annual deviation from the overall period mean for total June precipitation – note that the years 1992-1993; 1996 - 2001, and 2003-4 were all below-average for June precipitation. The years with both warmer and drier than average conditions in June were 1993, 1997, 1999, 2001, and 2004.  Table 1 shows that each of the three higher-than average cone production years in the Forest site were initiated in a June with a combination of warmer than normal temperatures and drier-than normal precipitation sums.

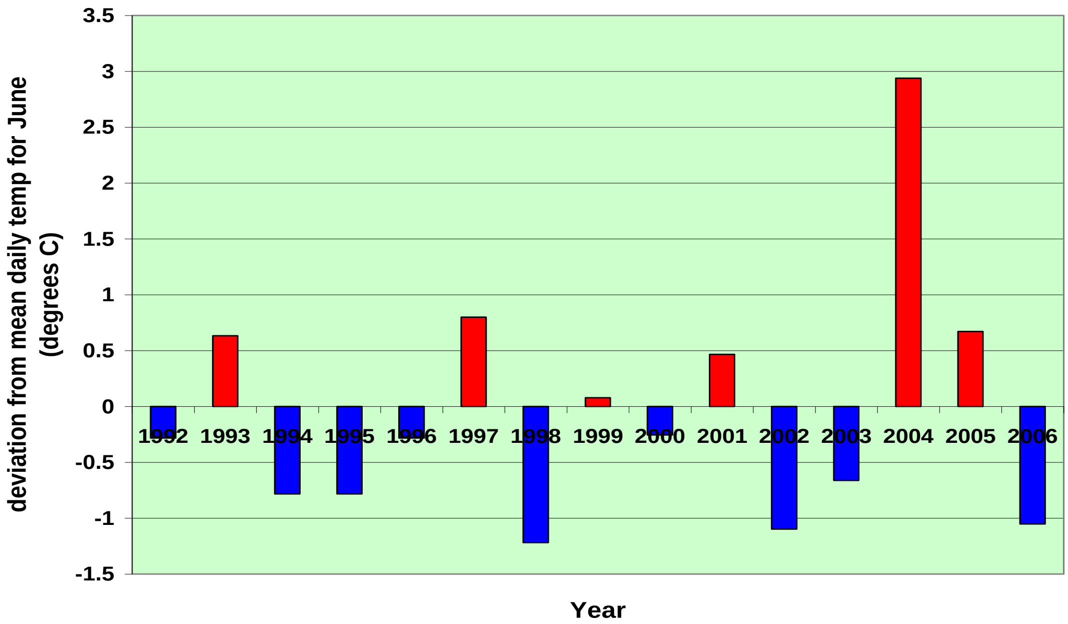


Figure 14. Histogram showing the deviation from mean average daily June temperature for each year during the period 1992 – 2007. Years with above-average mean daily June temperatures are indicated with red bars, years with below-average mean daily June temps are represented by blue bars. The mean daily temperatures for the month of June were above average in 1993, 1997, 1999, 2001, 2004, and 2005.

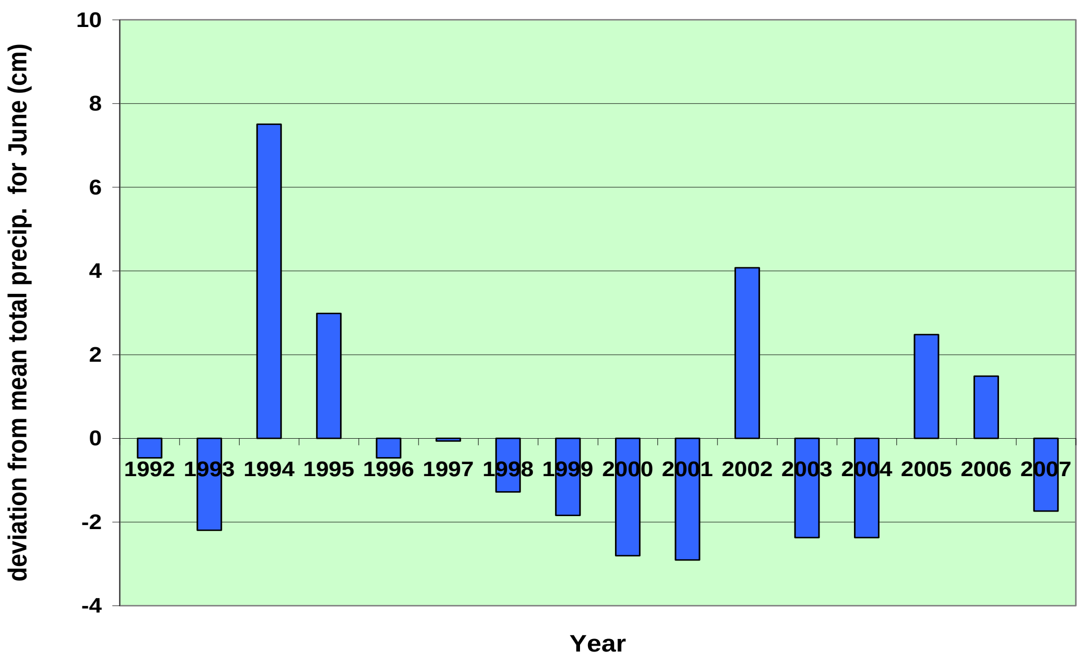


Figure 15. Histogram showing the deviation of the annual amount of precipitation for June from the grand mean of June precipitation for each year during the period 1992 – 2007 at Denali NP headquarters weather station.

Above-average cone crops that were observed in the Forest site over this period were initiated in 1997, 1999, and 2001 (see Fig. 11) – note that each of these years had both above-average June daily temperatures, and below-average June precipitation totals for the period (see Figs. 14 & 15 and Table 1). Above-average cone crops in the Treeline site were initiated in the years 1992, 1997, 1999, 2003, and 2004 (Fig. 12; Table 2). During each of these years, the Park headquarters area experienced both below-average precipitation and above-average temperatures except for 1992 and 2003. June 2003 was the third driest June over this period, but experienced below average daily maximum June temperatures in comparison to the entire period. It is worth noting that 2003 was a conspicuous outlier in terms of the very low mean depth of the snowpack in spring, thus likely exacerbating the degree of drought experienced by study trees in June because snowmelt occurred very early in relation to other years in this period (see Figs. 4 & 5). In fact, 2003 was the only year in the period with snow-free-days in the month of April at Park HQ.

Table 1. Table summarizing the relationship between the initiation of large cone crops and early-season weather conditions for the Forest plots in the Rock Creek drainage. The years 1992-2006 are represented by the columns in this table.

| | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 00 | 01 | 02 | 03 | 04 | 05 | 06 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| June DD | - | + | - | - | - | + | - | + | - | + | - | - | + | + | - |
| June Precip | - | - | + | + | - | - | - | - | - | - | + | - | - | + | + |

++ Green cells signify years in which larger-than-average white spruce cone crops were initiated in the Forest site of the Rock Creek watershed monitoring plots. Plus signs indicate that the year had higher than average mean for the climate parameter in questions (number of degree days in June, or cumulative cm of precipitation in June).

Table 2. Table summarizing the relationship between the initiation of large cone crops and early-season weather conditions for the Treeline plots in the Rock Creek drainage. The years 1992-2006 are represented by the columns in this table.

| | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 00 | 01 | 02 | 03 | 04 | 05 | 06 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| June DD | - | + | - | - | - | + | - | + | - | + | - | - | + | + | - |
| June Precip | - | - | + | + | - | - | - | - | - | - | + | - | - | + | + |

++ Green cells signify years in which larger-than-average white spruce cone crops were initiated in the Forest site of the Rock Creek watershed monitoring plots. Plus signs indicate that the year had higher than average mean for the climate parameter in questions (number of degree days in June, or cumulative cm of precipitation in June).

In June 1993 the headquarters of Denali area experienced both above average temperatures and below-average precipitation, suggesting that the cone crop that was initiated in 1993 and came to maturation in 1994 should have perhaps been a relatively large one. However the mean numbers of cones that were observed in 1994 for both of the Rock Creek Treeline and Forest sites were both below average (see Fig 11). An important factor likely affecting cone initiation in 1993 was the physiological status of the trees – the period 1992-1993 was a highly stressful one with very short growing seasons (particularly in 1992) possibly resulting in the trees having low reserves that were insufficient to stimulate production of large numbers of cones. The nutritional reserves and physiological status of trees is another important factor that determines the size of a given year’s cone crop.

***White spruce seed rain***

The average number of white spruce seeds per trap ($0.25m^2$) per year for the Forest site ranged from a low of 2.4 seeds/trap in 1995 to a high of 471 seeds/trap in the banner cone year 1998, yielding a range in the average annual seed rain of 468.6 seeds/$0.25m^2$ (Fig. 16). The average number of seeds per trap per year for the Forest site across the entire period was 71.5 (± 31.4). In only three of these years was the number of seeds per trap higher than the mean over the entire period of 1998, 2000, and 2002. The number of seeds per trap in the Forest site was particularly low (that is, less than 10 seeds per trap, on average) in the years 1993, 1995, 2003, 2004, and 2006. As expected, the annual variation in the size of the white spruce seed crop were highly positively correlated with the variation in estimated cone production (r = 0.871; Fig. 17).

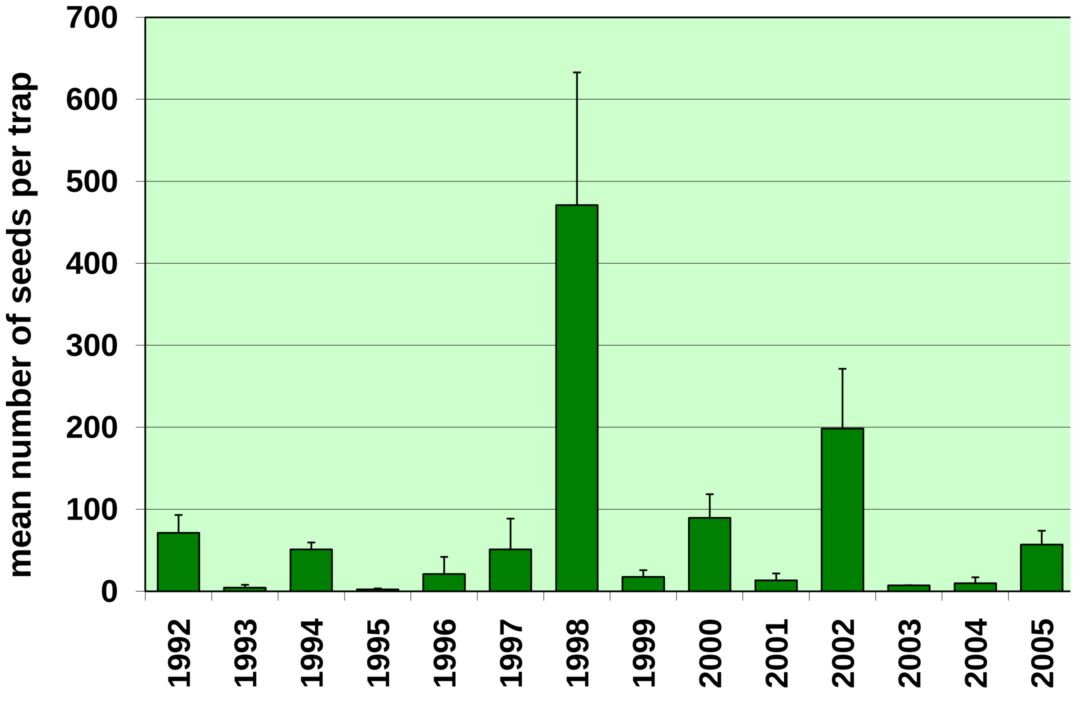


Figure 16. Histogram showing the mean number of seeds per trap in the Forest site of the Rock Creek drainage over the period 1992-2006 (± 1 se).

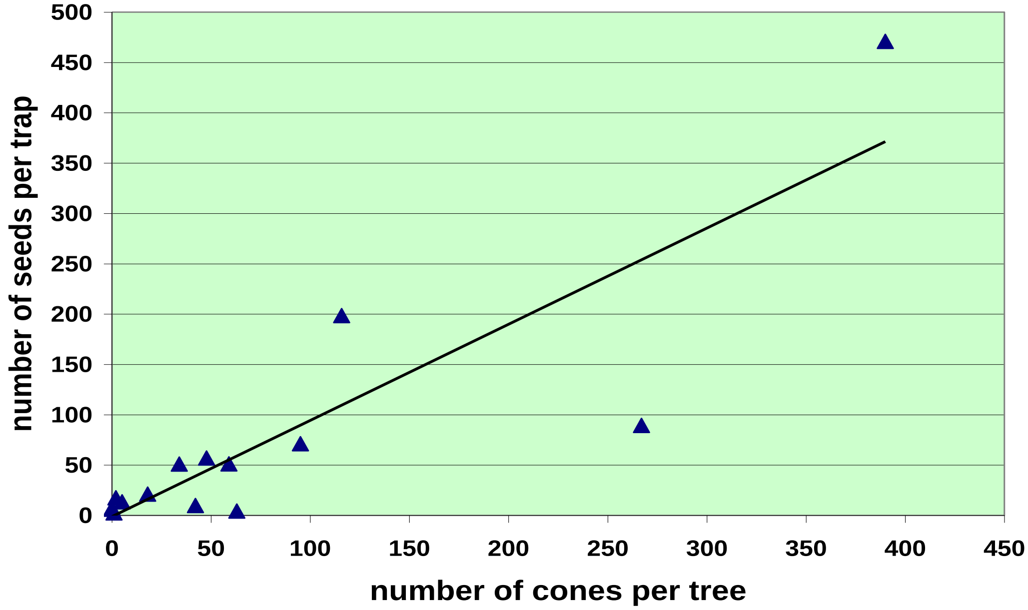


Figure 17. Correlation between annual estimates of cone and seed crops in the Forest site of the Rock Creek drainage long term monitoring plots.

The average number of white spruce seeds per seed trap per year for the Treeline site ranged from a low of 0.3 seeds/trap (observed in 1993, 1995, and 1996) to a high of 18.3 seeds/trap (observed in 2005) for a range in average seed rain of 18 seeds/0.25m$^2$ per year over the period for this site (Fig. 18). The average number of seeds per trap per year for the Treeline site across the entire period was 4.4 (± 1.4). The number of seeds per trap in the Treeline site was greater than 10 seeds/trap in only two years - 1998 and 2005 (not coincidentally also the two largest cone crop years over the period). The number of seeds per trap in the Treeline site was particularly low (less than 1 seed per trap, on average) in 1993, 1995, and 1996). However, it should be noted that the Treeline seed count data are subject to relatively large sampling error (and potential bias) because of the much higher potential for seeds to be redistributed by wind in this landscape position. The lower-stature of the vegetation and greater exposure to higher wind speeds in the Treeline site likely complicate the efficacy of the seed traps there relative to the Forest site. Thus the correlation between annual cone crop estimates and mean number of seeds per trap for the Treeline site was lower than was observed for the Forest site ($r = 0.656$; Fig. 19).

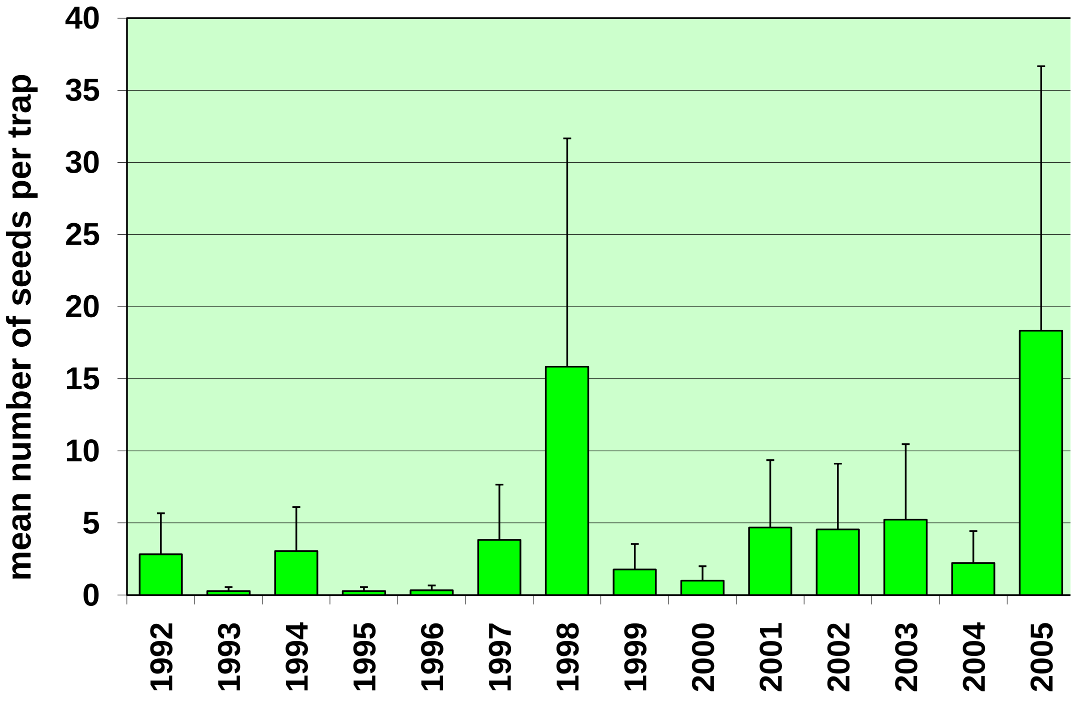


Figure 18. Histogram showing the annual variation in the number of seeds per seed trap collected in the Treeline site of the Rock Creek drainage in Denali National Park.

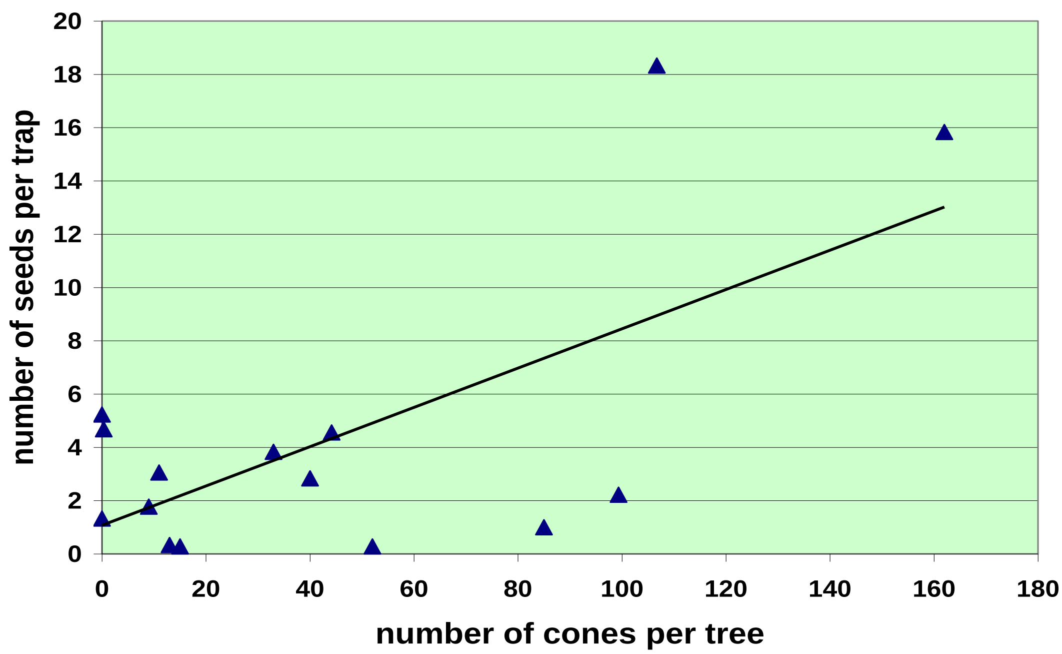


Figure 19. Correlation between annual estimates of cone and seed crops in the Treeline site of the Rock Creek drainage long term monitoring plots.

There are both similarities and differences in the patterns of annual variation in seed rain between the Forest and Treeline sites in Rock Creek over the course of this study. Specifically, the pattern of variation in the relative size of the seed crop (as measured by the mean number of seeds per trap) appeared to be largely synchronous in these two sites for the years 1992-1999 (see fig. 20). However, this synchrony in relative size of the seed crop apparently diminished in the years 2000-2006, especially in 2005 when the Treeline seed crop was 419% of the Treeline mean over the period and the Forest seed crop was 80% of the Forest mean for the period (Fig. 20). In general, there appeared to be a trend towards relatively larger seed crops in the Treeline site and relatively smaller seed crops in the Forest site in the later period after 2000. The exception to this pattern was 2002 during which the mean number of seeds in the Forest seed traps was 280 % of the mean over the periods as compared to Treeline site where the number of seeds per trap was just 104 % of the mean for that site over the measurement period.

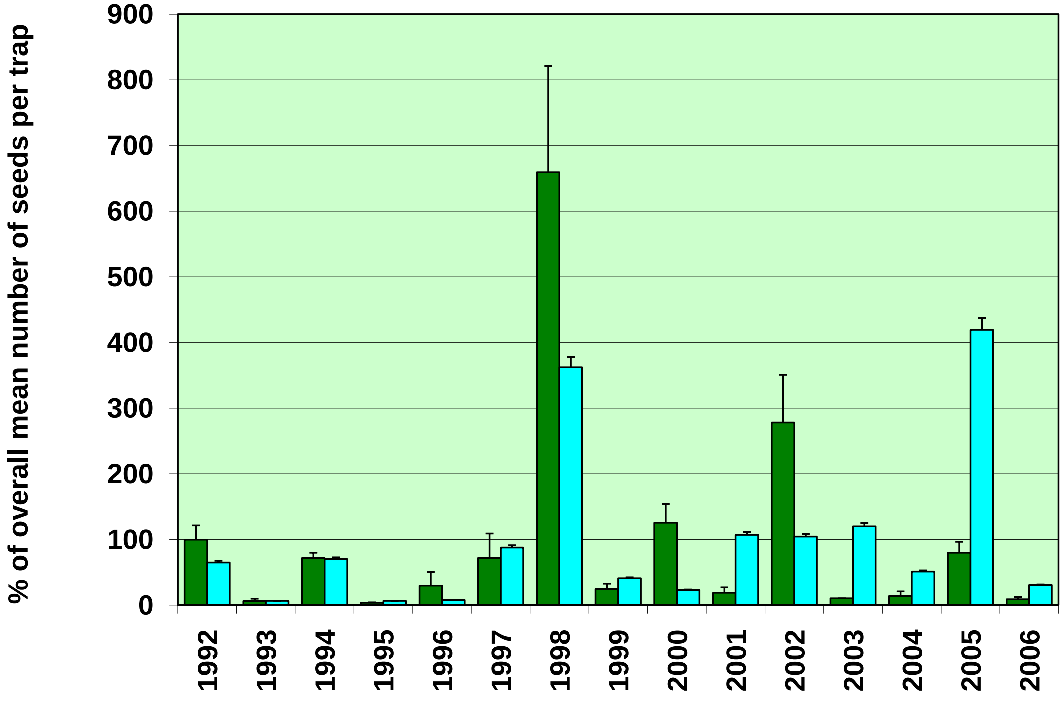


Figure 20. Histogram showing the annual variation in the number of seeds per seed trap (standardized by the grand mean for each site) in the Forest and Treeline sites of the Rock Creek drainage in Denali National Park. Value shown is the percent of the overall mean across the period reflected by the annual value for each year at each site. Thus, the number of seeds observed in the Forest site in 1992 was 71.2 seeds per trap, or 99.7% of the overall mean of 71.5 for the Forest site across all years measured.

### *Comparisons of Rock Creek and Bonanza Creek LTER seed rain*

To compare our results with nearby observations of white spruce seed rain (recorded according to the same protocols), I have summarized the results available for seed rain monitoring in the floodplain white spruce forest stands at the Bonanza Creek Experimental Forest LTER site south of Fairbanks (data only available until 2003; see Figs. 21 and 22). It appears from this comparison that general pattern of annual variation in spruce seed rain among years over the period 1992-2003 for the floodplain white spruce forest sites in Bonanza Creek were substantially similar to those observed in the Rock Creek Forest site. Specifically, the three years with highest average white spruce seed rain were the same in both the Rock Creek Forest site and the Bonanza Creek floodplain plots (1998, 2000, and 2002). In addition, three of the four years with the lowest average number of seeds per trap were the same among these two sites as well (1995, 1993, and 2003). Indeed, the coefficient of simple correlation in the mean number of seeds per trap over this periods between these two sites was r = 0.867 (Fig. 22). This high degree of correlation between these two sets of seed rain values strongly suggests that seed productivity at the two sites was highly synchronous over the period. Furthermore, it's worth noting that the coefficient of correlation between these two sites was a substantially stronger than was observed between the neighboring Forest and Treeline localities within Rock Creek (r = 0.60).

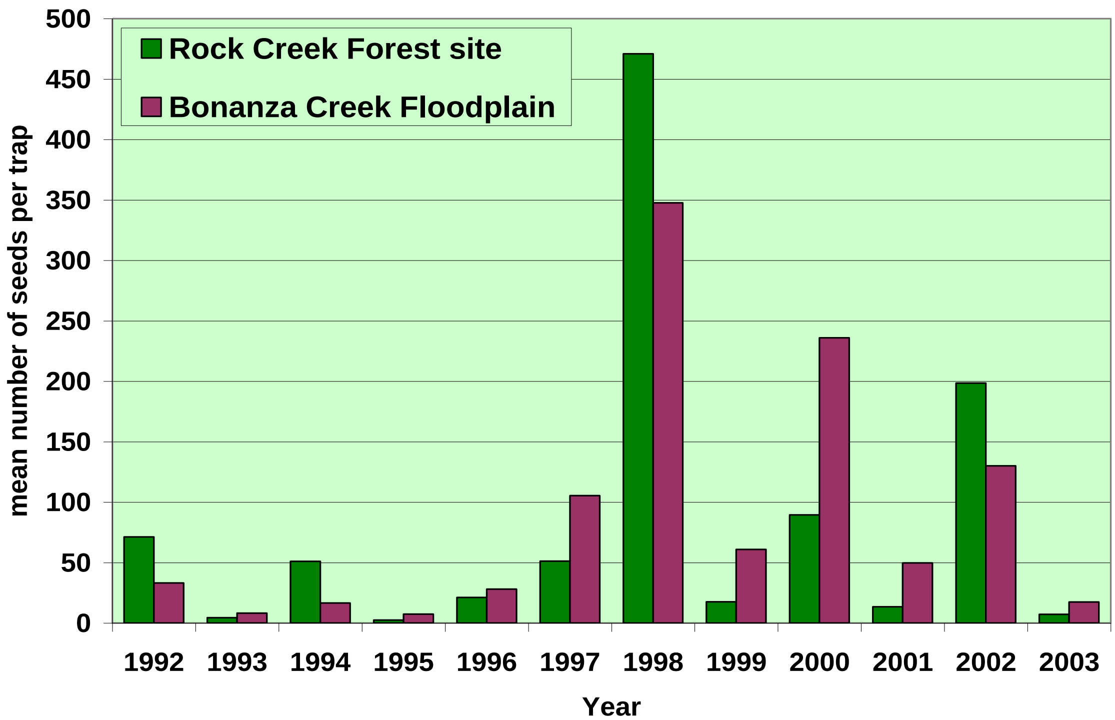


Figure 21. Histogram showing a comparison of the annual seed rain (the mean number of white spruce seeds in .25m$^2$ seed traps) in the Rock Creek Forest site and the Floodplain stands in the Bonanza Creek Experimental Forest Site near Fairbanks for the period 1992-2003.

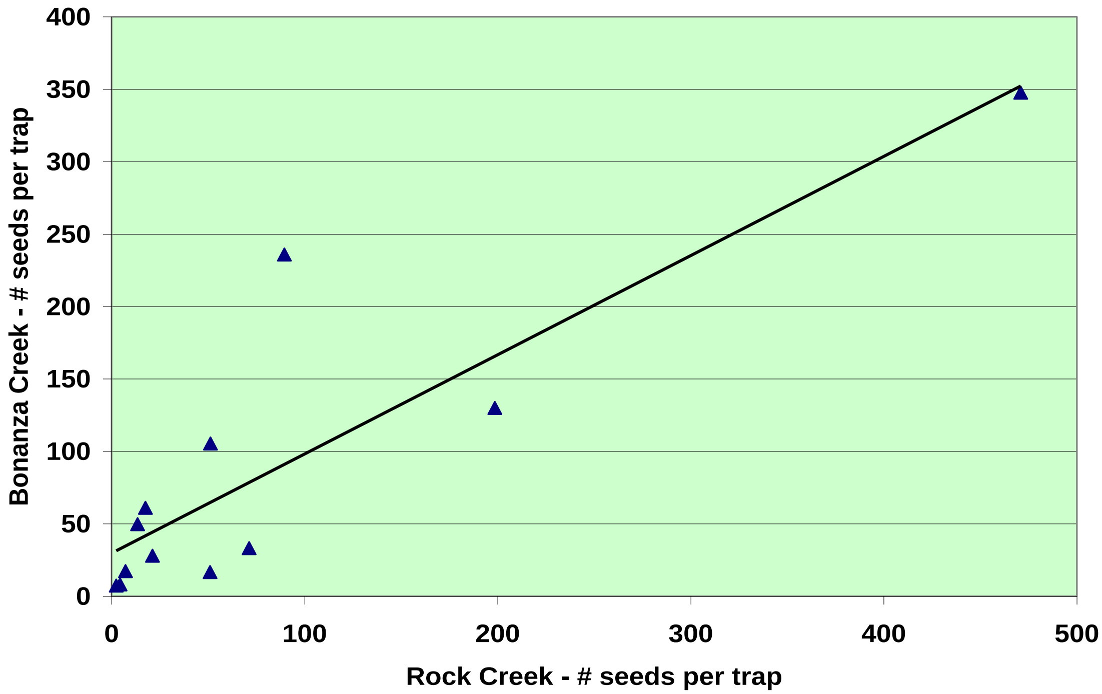


Figure 22. Correlation between the mean number of white spruce seeds per trap observed in the Rock Creek Forest and Bonanza Creek floodplain forest plots on an annual basis over the period 1992 – 2003.

***White spruce seed viability***

Seed germination trials were conducted each year to determine the viability of the white spruce seeds that were collected from the seed traps each year. I present these viability results both in terms of the mean germination *percentages* by site and mean *numbers* of viable seeds produced per trap per year. The number of seeds produced and the viability of this seed crop in any given year are for the most part independent of each other. This is because cones are initiated one year and then come to fruition and mature in the following year. The overall number of seeds produced is most closely related to the size of the cone crop (which is controlled by plant physiological status and conditions in the cone initiation year, one year prior to seed formation) and the viability of the seed crop that is ultimately produced is a function of plant physiological status and growing season conditions in the year they reach maturity.

Germination rates: The grand mean for germination percent of white spruce seeds over the entire measurement period was 9.1% for the Forest site (± 2.9%). The two highest mean annual germination percentages for the Forest site over this measurement period were 31% in 1997 and 28 percent in 2002 (Fig. 23) whereas no germination for seeds collected was recorded in the Forest site for the following years: 1992, 1993, 1995, 1996 and 1999 (Fig. 23). The grand mean for germination percent of white spruce seeds over the entire measurement period was 4.1% for the Treeline site (± 1.96%). For the Treeline site, the two highest mean germination percentages observed over the measurement period were 23% in 2005 and 12 % observed in 2002 (Fig. 23).

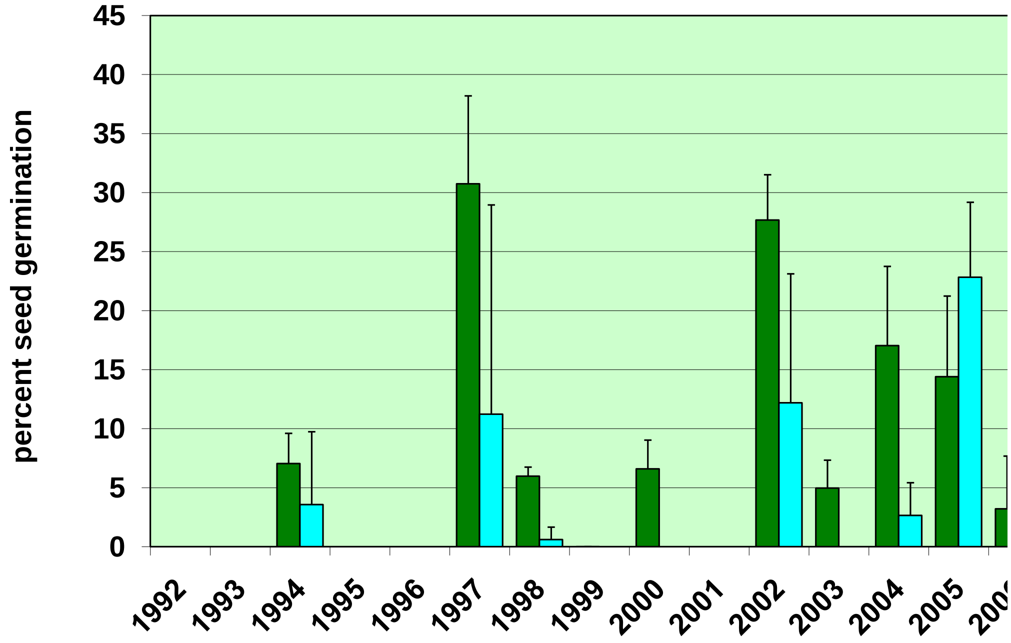


Figure 23. Mean germination percent (seed viability) observed for white spruce seeds collected in the Forest and Treeline monitoring sites in Denali National Park and Preserve during the years 1992 – 2006.

A comparison of the values for mean annual germination percentage for each site standardized by their respective grand means, shows that the years with higher-than-average germination percentages were very similar: 1997, 2002, 2004, and 2005 for the Forest site and 1997, 2002, and 2005 for the Treeline site (Fig. 24).

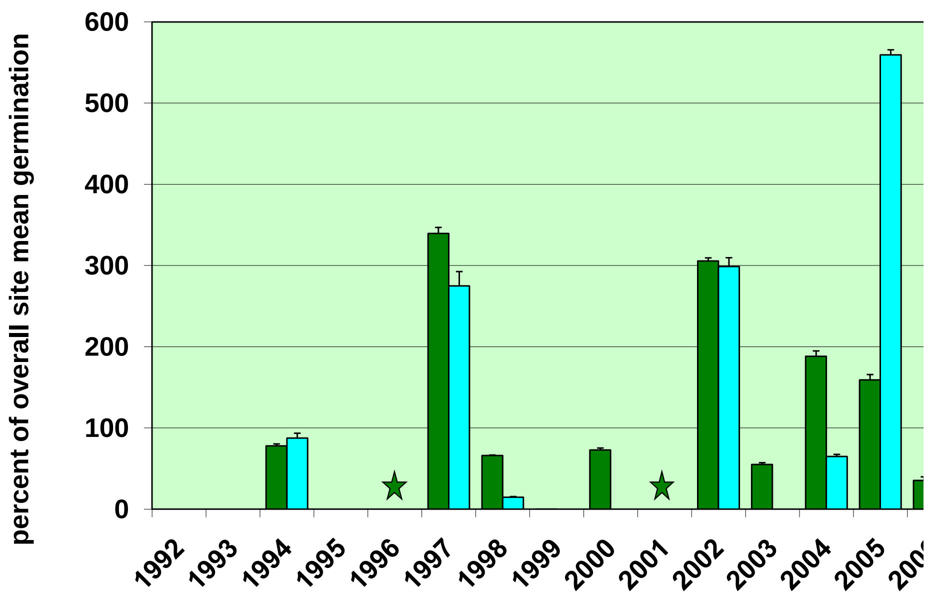


Figure 24. The percent of the overall mean germination percentage for each site for each year in the period at two monitoring sites in the Rock Creek drainage of Denali National Park. Stars indicate missing data.

Size of viable seed crop: The number of viable (germinated) seeds per trap (or by extension, per unit land area) is a function of both the numbers of seeds and the relative viability of the seed crop produced in a given year ([total # seeds per trap] x [% viability] = # of viable seeds per trap). This is an informative statistic because it reflects the true capacity of the seed crop from a particular year to result in the establishment of new tree seedlings and recruitment into the population of white spruce on the landscape. It is worth noting that we observed years with relatively highly ‘productive’ seed crops that had relatively low viability (notably that of the banner cone crop of 1998) and years in which trees produced relatively low numbers of seed but relatively high germination percentages that resulted in larger viable seed crops (compare Figs. 14 and 15 with Fig. 24).

The number of viable seeds per trap was variable both between sites and among years in the Rock Creek drainage (Fig. 25). The mean number of viable seeds per trap for the Forest site over the period was 8.59 viable seeds per trap (± 4.38) whereas the overall mean for the period for the Treeline site was 0.41 viable seeds per site (± 0.27). This reflects both the higher seed production and the greater viability observed in the low elevation Forest trees as compared to the spruce in the Treeline site. In the Forest site, the highest mean number of viable seeds observed during this period was 54 viable seeds per trap which was recorded 2002 (Fig. 25). It is remarkable that this value was twice the number of *viable* recorded in the banner cone year of 1998, even though there were more than twice as many cones and seeds produced in 1998 as compared to 2002. For the Treeline plots the highest number of viable seeds was 3.6 per trap, also recorded in 2005.

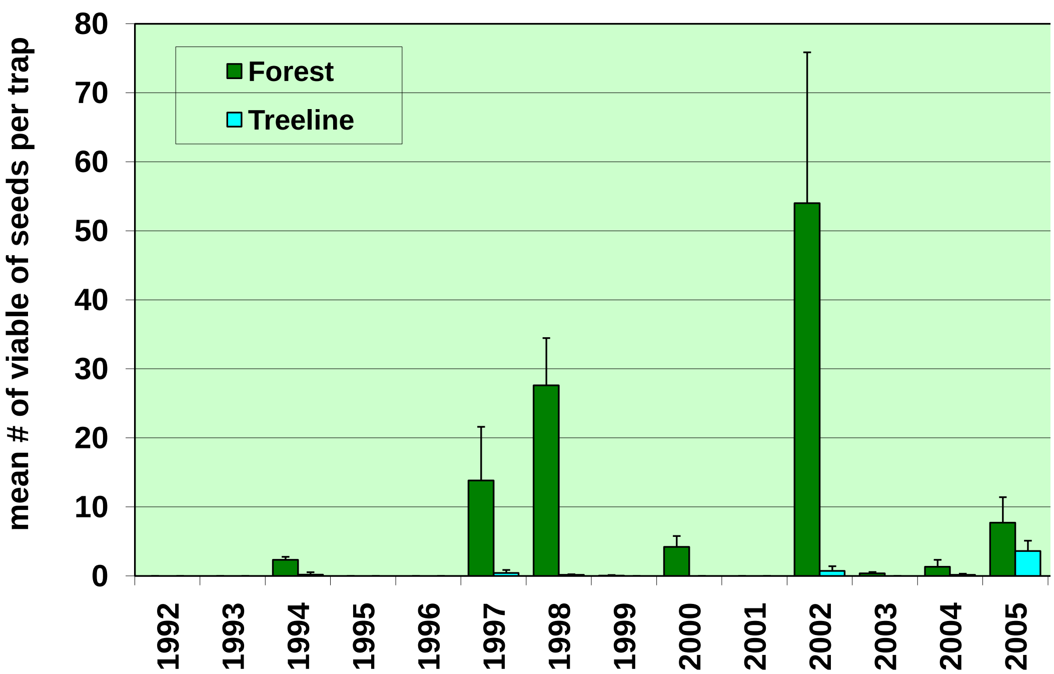


Figure 25. Histogram showing the annual variation in the mean number of viable white spruce seeds per trap in the Forest and Treeline monitoring sites in the Rock Creek drainage of Denali National Park over the period 1992 – 2006.

The white spruce trees in the Forest site apparently produced higher numbers of viable seeds, on average, than the trees in the Treeline site over the course of this study. Indeed, 2005 was the only year where appreciable numbers of viable seeds were collected in the Treeline site seed traps as compared to the Forest seed traps. This apparent difference between the two sites is due to three factors:

1) There have been consistently higher number of seeds produced (in general) by the larger trees in the Forest site on average over the course of this study
2) There has been apparently higher seed viability, on average, of seeds in the Forest site as compared to than the seeds from the Treeline site during this period; and,
3) There are differences in "trap-efficiency" between the seed traps in the Forest site versus the Treeline site. I believe that a higher percentage of the seeds that fall within the Forest are collected in the traps due to the windiness of the Treeline environment dispersing these seeds thus providing a somewhat biased estimate of the differences in seed rain between the two sites.

It is interesting to note that the pattern in production of viable seed varies in important respects from the pattern of cone production in both sample sites. Specifically, 1998 was a banner cone year for white spruce across interior (and perhaps all of) Alaska, with large numbers of cones and seeds produced. This phenomenon was noted by many people across the state at the time. However, these data suggest that during at least one other year in which fewer cones were produced per tree (on average) many more viable seeds were actually produced than during the banner cone crop of 1998. Specifically, average cone production per tree in the Forest site in 1998 was more than twice the average for 2002 (199 cones per tree in 2002 vs. 471 cones per tree in 1998) but the average number of viable seeds per trap observed for this site in 2002 was double the 1998 average (54 seeds per trap in 2002 vs. 27.3 in 1998). Similarly, in 1998 the average number of cones per tree in the Treeline site was 162, twice the mean of 73 cones per tree that were observed in 2002. In contrast, there were only 0.17 viable seeds per trap observed in 1998 as compared to 0.72 viable seeds per trap recorded in 2002.

This apparent discrepancy between reproductive effort (cone production) and potential reproductive success (production of viable seeds) has important consequences for these populations because substantial energy reserves are allocated to cone production by white spruce. That this discrepancy is possible is due to the two-year cycle of seed production in white spruce. A large cone crop may be initiated in one year as conditions favor it (for example, the warm, dry June of 1997) but conditions in the second year may not be optimal for the production of large numbers of viable seeds (for example in the relatively, short, cool growing season of 1998).

### *Relationships between white spruce seed viability and climate variables*

There was a weak positive correlation between the number of degree days accumulated after the snow-free date for the growing season in a given year and the germination percentage of white spruce seeds collected in the Forest site for that year ($r = 0.26$; see Fig. 26). High viability percentages for the Forest site were observed in 1997, 2002, 2004, and 2005 (Table 3). The two visible outliers in the relationship between seed germination and degree days were 1997 and

2002. In both of these years relatively high precipitation sums were recorded at the Park Headquarters weather station.

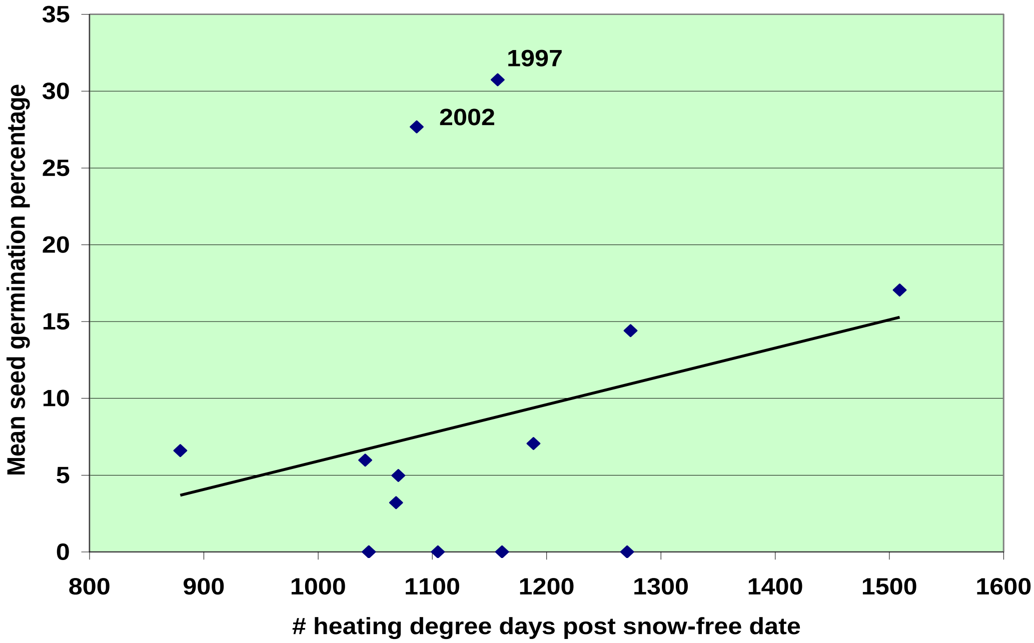


Figure 26. Scatterplot showing the relationship between the sum of cumulative heating degree-days post-snow free date and mean annual germination percentages for white spruce seeds collected in the Forest site of the Rock Creek study area in Denali National Park during the period 1992-2006. Two conspicuous outliers are labeled by year.

Table 3. Table summarizing the relationship between the average viability of white spruce seed crops and growing-season weather conditions for the Forest site in the Rock Creek drainage. The years 1992-2006 are represented by the columns in this table.

| | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 00 | 01 | 02 | 03 | 04 | 05 | 06 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Total GS DD** | - | + | + | + | - | + | - | - | - | - | - | - | + | + | - |
| **Total GS Precip** | - | - | - | + | - | + | + | - | + | - | + | - | - | + | + |

++Green cells signify years in which white spruce seeds collected in the Forest plot had higher-than-average germination percentages. Plus signs indicate that the year had higher than average mean for the climate parameter in question (number of degree days in the period April – August, or cumulative cm of precip. in April through August).

There was also a weak positive correlation between annual mean germination percentages and the number of snow-free degree days for a year for the Treeline site ($r = 0.296$; see Fig. 27). Mean germination percentage was above average for three of the years in the measurement period at the Treeline site: 1997, 2002, and 2005 (Table 4). We observed higher-than-average germination for each of these years in the Forest site as well. In addition, the positive outliers for the Treeline data set were similar to those observed for the Forest site for this relationship – 1997, 2002 and 2005. Interestingly, each of these years experienced above-average precipitation across the growing season (Fig. 27).

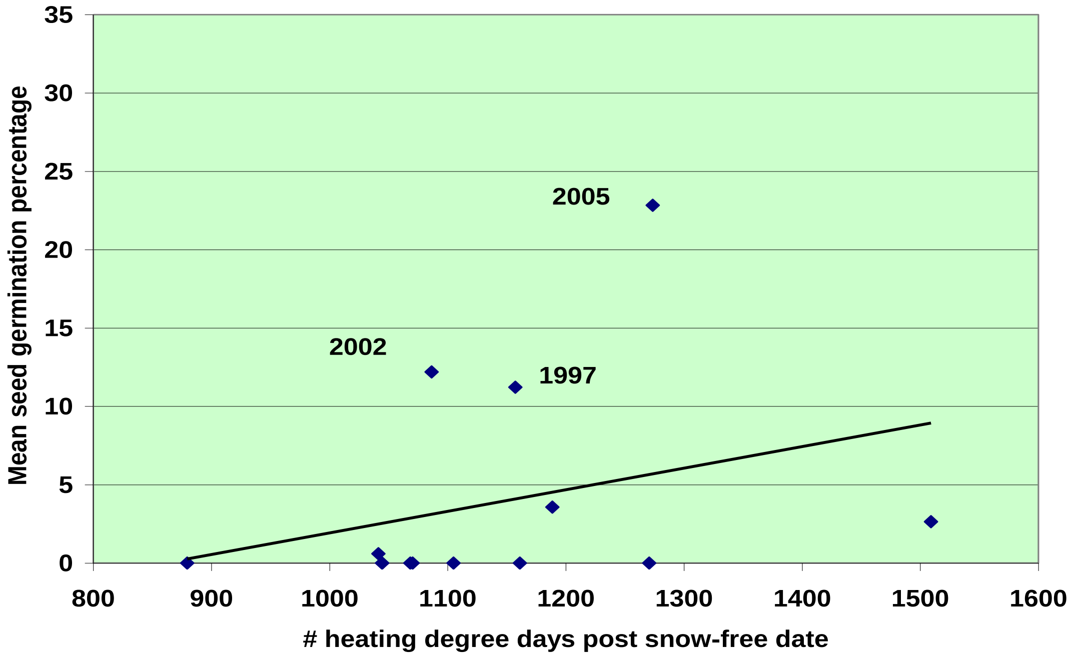


Figure 27. Scatterplot showing the relationship between the sum of cumulative heating degree-days post-snow free date and mean annual germination percentages for white spruce seeds collected in the Treeline site of the Rock Creek study area in Denali National Park during the period 1992-2006. Three conspicuous outliers are labeled by year.

Table 4. Table summarizing the relationship between the relative viability of white spruce seed crops and growing-season weather conditions for the Treeline site in the Rock Creek drainage.

| | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 00 | 01 | 02 | 03 | 04 | 05 | 06 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Total GS DD** | - | + | + | + | - | + | - | - | - | - | - | - | + | + | - |
| **Total GS Precip** | - | - | - | + | - | + | + | - | + | - | + | - | - | + | + |

++Green cells signify years in which white spruce seeds collected in the Forest plot had higher-than-average germination percentages. Plus signs indicate that the year had higher than average mean for the climate parameter in question (number of degree days in the period April – August, or cumulative cm of precip. in April through August).

At the latitude of Denali, an important factor limiting white spruce seed viability is cumulative warmth over the growing season - that is, that the trees physiological growth requirements are met by accumulating enough degree-days to produce fully viable seed crop. These results suggest that warm years may indeed result in an increase in the viability of the seed crop in this study area along with other factors.

***Comparisons of Rock Creek Forest and Bonanza Creek white spruce seed viability***

The mean percent seed germination of white spruce seeds (viability) observed in the floodplain white spruce forest plots of the Bonanza Creek LTER site over the period 1992 – 2003 was 11 % which was slightly higher than the mean overall germination percentage observed in the Rock Creek Forest plots over the same period, which was 9.1 % (see Fig. 28). Furthermore, the values for annual germination percentages between the two sites were positively correlated (r = 0.67; Fig. 29). Two exceptions to the general synchrony in seed viability between these two sites were observed in the years 1992 and 2004 during which the germination percentages for the two sites were substantially different. The germination percent in 1992 was very high for the Bonanza Creek sites but was zero for the Rock Creek Forest site whereas in 2002 the germination percentage of seeds collected in the Rock Creek Forest was apparently higher, on average, than was observed in the Bonanza Creek plots (28 % vs. 18%).

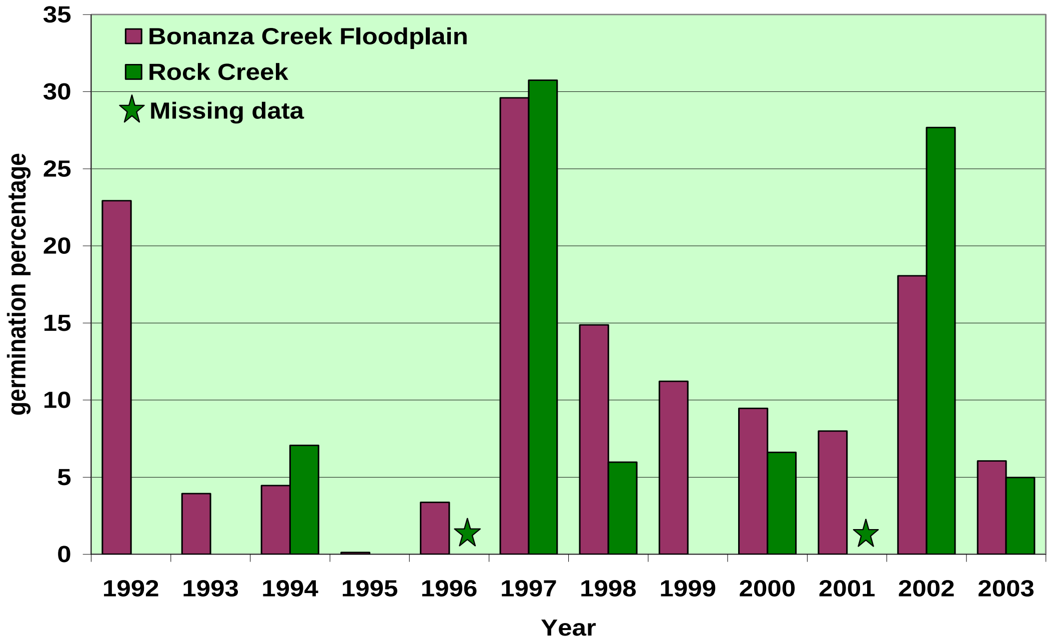


Figure 28. Germination percentages of white spruce seeds collected in seed traps in two study areas in the boreal forest of interior Alaska – Rock Creek drainage Forest site in Denali and the Floodplain white spruce forest stands in the Bonanza Creek Experimental Forest near Fairbanks.

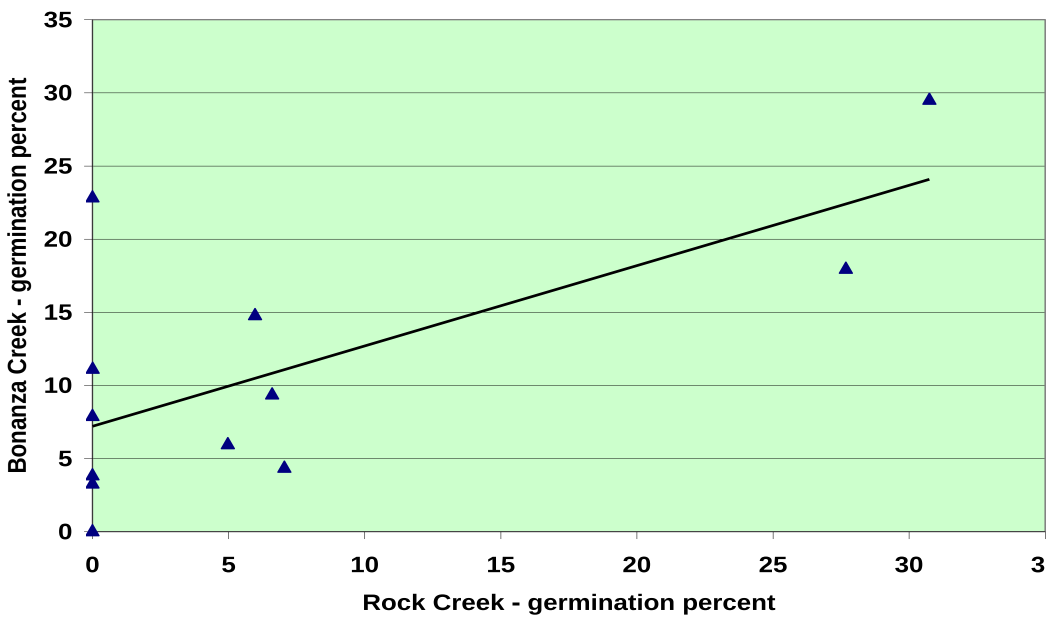


Figure 29. Scatterplot showing the relationship between germination percentages of white spruce seeds observed in the Rock Creek Forest site and those recorded for the Bonanza Creek floodplain forest during the period 1992 – 2003.

In general, the pattern in relative seed viability and overall production of viable seeds per unit area within this data set suggests decreasing mean seed viability and viable seed productivity with increased site elevation with the following order: Bonanza Creek floodplain > Rock Creek Forest > Rock Creek Treeline. This likely reflects the influence of season length and warmth (degree-day sums) in stimulating the production of viable white spruce seeds at this latitude. However, in particularly warm years such as 2004 and 2005, the percent viability of the seeds collected from the Treeline site may approach the levels observed in the other two sites. In short, cool summers (such as 1992, 1996, 1998, 2000, 2003 and 2006) there was virtually no viable seeds produced in the Treeline white spruce according to these data.

***Annual variation in winter resident finch counts and small mammal density estimates in relation to white spruce seed crops***

White spruce and mixed spruce-birch forests are an important vegetation type in Denali National Park, perhaps the most productive forest type in terms of annual primary productivity and standing crop. Because of their large numbers and concentration of food resources, white spruce seeds can represent a major resource for a variety of birds and mammals.

To examine the possibility that the strong variation in the inter-annual productivity of white spruce may be synchronous with population levels of local birds and animals for which we have data, I compared the spruce seed data with counts of winter resident birds that use spruce seeds as a food resource (white-wing cross-bills, common redpolls and pine grosbeaks) and population data for red-backed voles. The bird data come from the annual Audubon Christmas bird count conducted each year at the east end of Denali (in close proximity to the Rock Creek study area) and the vole data come from the long term trapping grid that is co-located with the spruce monitoring plots in the Rock Creek drainage.

There is apparently very strong synchrony between the relative numbers of white-winged crossbills counted during the Denali Christmas bird count and the number of white spruce seeds per trap recorded in the Forest site over the period 1992-2006 (Fig. 30). Indeed, the coefficient of simple correlation among these two values over this period was $r = 0.952$, reflecting an extremely strong positive correlation between these two sets of values (Fig. 31a). Apparent synchrony in numbers of common redpolls with the seed crop was also observed, although to a lesser degree than for the crossbills (Fig. 31b; $r = 0.750$). Numbers of pine grosbeaks recorded during the Christmas bird count and density of red-backed voles in the Forest site did not appear to be correlated with white spruce seed rain in this data set (see Fig. 31c and 31d; correlation coefficients of $r = -0.017$ and $-0.166$ respectively).

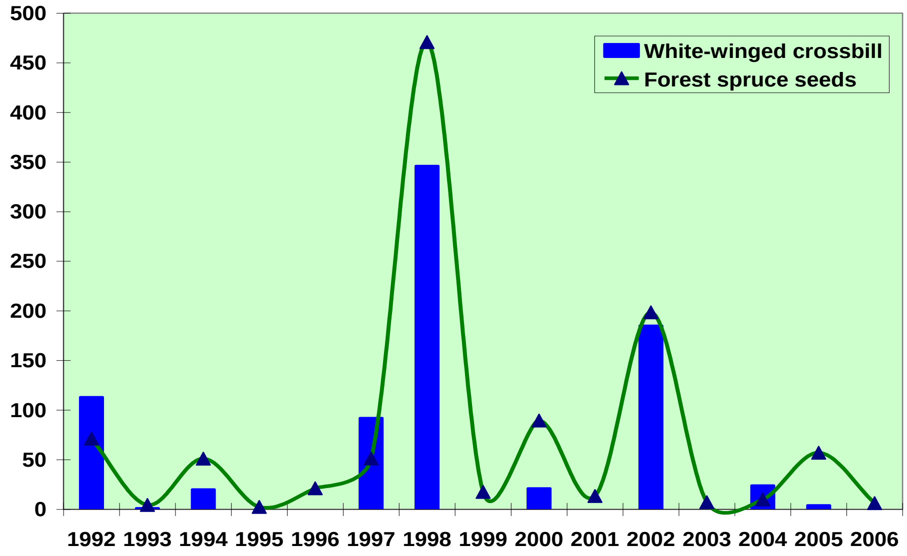


Figure 30. Histogram showing the pattern of apparent synchrony in the mean number of white spruce seeds per trap in the Forest site in the Rock Creek drainage and the number of white-winged crossbills observed during the annual Christmas bird count in Denali for the period 1992-2006.

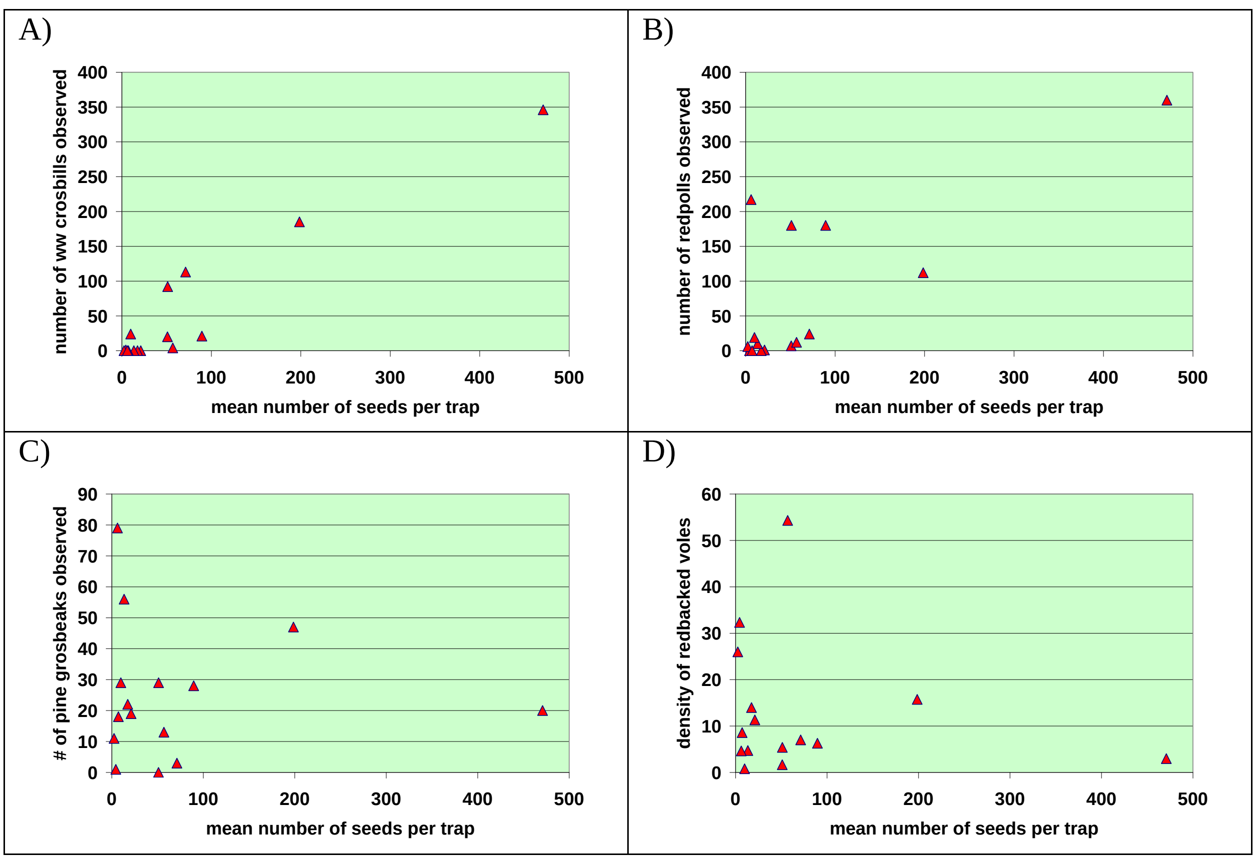


Figure 31. Four scatter-plots showing the relationship between the mean annual number of white spruce seeds per trap recorded in the Rock Creek Forest monitoring site and annual counts and density estimates for three bird species (Christmas Bird count data): A) crossbills; B) redpolls; C) pine grosbeaks; and D) red-backed vole densities for each year during the period 1992-2006.

# Discussion

The primary objective for the establishment of the vegetation monitoring plots in the Rock Creek watershed in 1992 was primarily to monitor the effects of global warming on the subarctic vegetation mosaic along a gradient of elevation. One overarching question at the foundation of this program was: would treeline move to higher elevations as spruce trees invaded newly habitable areas of the landscape in response to warmer temperatures and longer growing seasons? To this end, plots were installed in forest, treeline and tundra vegetation to quantify the vegetation of these areas for future comparisons to detect change. Because white spruce is the primary treeline species in this area, considerable focus was placed on quantifying the response of this species over time. Presumably, colonization of new areas of the landscape would be presaged by increases in the reproductive performance of trees in treeline communities. Increasing reproductive success of treeline spruce trees would result in increased dispersal of seeds into the new areas (that is, contiguous patches of tundra vegetation).

After 16 years of carrying out the white spruce monitoring protocols, it is worth enquiring: what can we conclude about the patterns of white spruce growth and reproduction in this study area and the relationship between climate and white spruce reproductive effort along the elevation gradient based on this record? I provide a set of summary conclusions based on this data set below.

### Overall summary of white spruce cone and seed monitoring data

The white spruce monitoring effort over the period 1992-2007 has yielded a unique and important data set for understanding the reproductive performance of white spruce in interior Alaska over this period of time. The data set provides information about how reproductive effort in spruce has varied over time in relation to annual variation in climate and in relation to the landscape position of trees (e.g. boreal lowlands vs. treeline). Differences in the apparent responses in the reproductive performance of white spruce trees at Treeline versus closed Forest in relation to climate variability provide some potential insights into trajectories of change with climatic warming. The comparisons of our long term data set with that of the Bonanza Creek Experimental Forest has also yielded information on the spatial and temporal correlation of white spruce reproductive effort over a larger area of interior Alaska for this 16 year period.

While not necessarily conclusive from a statistical perspective, the results of sixteen years of white spruce monitoring in the Rock Creek drainage, and our comparisons to nearby areas (Bonanza Creek LTER) suggest the following conclusions:

- Annual cone production of white spruce trees in both Rock Creek study sites (Forest and Treeline) was extremely variable among years, with a few highly productive years and the majority of years with negligible cone production during the measurement period. 1998 was a banner cone crop at both spruce monitoring sites in the Rock Creek study area.

- The average number of cones per tree in white spruce was higher, on average, in the Forest site than in the Treeline site over the period: 71.2 ± 27.2 vs. 41.9 ± 11.2 respectively. However, in two recent warm summers (2004 and 2005) we observed higher mean cone productivity per tree in the white spruce at the Treeline site as compared to the trees in the Forest site.

- There was a relatively strong positive correlation in the pattern of annual variation in mean number of cones per tree (r =0.793) between the Forest and Treeline sites reflecting a general synchrony in cone productivity of trees in these two landscape positions.

- Based on the Rock Creek kennels weather station data, the three warmest growing seasons (as measured by the sum of heating degree-days accumulated post-snow free date in the period April – August) observed over the measurement period occurred in the last four years (2004, 2005 and 2007). 2004 and 2007 were also lower-than-average for the period in terms of growing-season precipitation sums.

- In the years 2004 and 2005 we recorded high levels of cone production by white spruce trees in the Treeline site but well below-average cone production for trees in the Forest site. This suggests different limiting factors may be operating on the trees at the two sites. Interestingly 2004 was the warmest year in the period by all measures (average temperature and degree-day accumulation). It is possible the lowland trees in closed Forest experienced a density-dependent drought stress as a result of this long, dry summer growing season. Treeline sites support much less dense stands and thus less competition among individual spruce trees.

- These results appeared to conform to the pattern of above-average cone crops being initiated in response to warm, dry conditions in the early growing season (June) that has been documented in the literature. Specifically, for the Forest site above-average cone crops were initiated in 1997, 1999, and 2001 – all years with higher than average June daily temperatures and below-average June precipitation. For the Treeline site, above-average cone crops were initiated in the years 1997, 1999, 2003, and 2004 - during each of these years, the Park headquarters area experienced both below-average precipitation and above-average temperatures except for 2003, which was the third driest June over this period, but experienced below average daily maximum June temperatures in comparison to the entire period.

- As expected, the relative abundance of cones in a given year was strongly positively correlated with seed rain for the Forest site, as measured by the seed traps. A similar correlation (although weaker) was observed in the Treeline site. It is likely that redistribution of seeds by wind is a source of bias in our estimate of relative seed production for the Treeline site.

- Overall, the average number of white spruce seeds per seed trap was consistently much higher and more variable in the Forest site as compared to the Treeline site across the study period: 71.5 seeds/trap/year ± 31.4 in the Forest site versus 4.4 seeds/trap/year ± 1.4 in the Treeline site.

- We observed a strong degree of synchrony in the patterns of annual variation in white spruce seed rain in white spruce trees in the Rock Creek Forest site and those in the floodplain white spruce forest site in the Bonanza Creek experimental forest (near Fairbanks) over the period 1992-2003. This is strong evidence that patterns in white spruce seed production are very large in scale, perhaps synchronous over much of interior Alaska, at least among trees located in similar landscape positions.

- Annual estimates of relative spruce seed viability (germination percentage) varied over the period, but in a manner out of phase with cone and seed productivity. The highest mean annual germination percentages of white spruce seeds were recorded in 1997 and 2002 in the Forest site (31% ± 7% and 28% ± 4% respectively). For the Treeline Site, the highest mean annual germination percentage was recorded in 2005 at 23% ± 6%.

- The estimates of mean annual seed viability across the entire period were considerably higher in the Forest than the Treeline site. We observed an overall mean of nine percent seed viability over the period for the Forest site and just 4 percent mean viability in the Treeline site over this period.

- The inter-annual patterns in the relative viability of white spruce seeds among years were generally synchronous between the Rock Creek Forest site and Bonanza Creek floodplain forest study areas during the period 1992-2003 with the exceptions of the cool summers of 1992, 1998, and 1999, in which the relative seed viability observed in the lowland Bonanza Creek area was apparently considerable higher, on average, than in the Rock Creek Forest site. Overall, mean seed viability was marginally higher in the Bonanza Creek site as compared to the Rock Creek Forest site.

- In general, the pattern in seed viability within this data set suggests decreasing mean seed viability with increased site elevation with the following order: Bonanza Creek floodplain > Rock Creek Forest > Rock Creek Treeline. This likely reflects the influence of season length and warmth (degree-day sums) in producing viable seed crops at this latitude. However, in particularly warm years such as 2004 and 2005, the percent viability of the seeds collected from the Treeline site may approach the levels observed in the other two sites.

- The largest mean number of viable seeds per unit area per year in the Forest site were observed in 2002 (54 viable seeds per trap - 0.25 $m^2$), 1998 (28 viable seeds per trap) and 1997 (14 viable seeds per trap). The overall mean for annual numbers of viable seeds produced per trap was 9 ± 4.38 (for the Forest site and 0.4 ± 0.27 for the Treeline site. Significantly, 1998, the year in which the largest mean annual production of white spruce cones and seeds were recorded in both Rock Creek monitoring sites was not the year during which the largest number of viable seeds were produced in these sites. In contrast, the highest mean annual viable seed production in the Forest site was recorded in 2002, the wettest year on record and the highest mean annual production of viable seeds in the Treeline site occurred in 2005 the second year of the warmest two-year period during the study.

In this report I have summarized the results of sixteen years of white spruce monitoring work at two sites (Forest and Treeline) in the Rock Creek drainage of Denali National Park in the context of annual variation in climate. This data set included annual cone counts, estimation of total annual seed rain per unit area, the relative viability of each year's seed crop and the annual variation in total numbers of viable white spruce seeds per unit area. In addition, by making direct comparisons to observations of a subset of the same parameters measured in the Bonanza Creek Experimental Forest I have examined the spatial scale of the responses of white spruce trees to climate variables in central interior Alaska. The final element of this report describes some initial investigations on the influence of the strong inter-annual variation in white spruce reproductive effort on other elements of the ecosystem. Specifically I compared annual count data for three winter-resident bird species known to utilize spruce seeds as a food resource (white-winged crossbills, common redpolls, and pine grosbeaks) and annual density data for redbacked voles to our estimates of white spruce seed production to determine

**Synchrony between winter-resident bird counts and spruce seed production**

Comparison of annual variations in white-winged crossbill counts with annual seed rain data from the Forest site showed a strikingly high degree of synchrony between these two variables during the course of this study. Variation in the annual count of common redpolls also showed marked positive correlation with the seed rain, although less than for the crossbills.The patterns in inter-annual variation of these two independent ecosystem attributes co-vary so closely to suggest that the size of each year's white spruce cone crop is perhaps the primary factor that influences the number of overwintering crossbills and common redpolls in this area of the Park. This long term data set documents a close relationship between annual variations in resident bird numbers based on food availability and is perhaps unique in interior Alaska. This information provides an important insight into the function of one level of trophic interactions in the ecosystem, but also an important tool for monitoring in the future. For example, if we observe departures in the close synchrony between white-winged crossbill counts and the white spruce seed crop in the future, it will be an indication of potential marked changes in the winter-resident crossbill population dynamics in this area.

The results of this 16 year monitoring program provide a dataset that illuminates one strand of the multi-trophic level set of interactions within the boreal ecosystem of interior Alaska over nearly two decades. This data stream includes the information about the influence of climate on stimulating annual variations in reproductive effort in white spruce, and the consequences of these variations for white-wing crossbills, a species dependent on spruce seeds for sustenance. This set of baseline of information will allow us to understand the potential perturbations to these ecosystem relationships that may occur due to warming climatic conditions in the boreal regions which will likely have profound influences on each level of this food chain.

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